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TROPICAL FORESTS: CONSERVATION AND USES

A SYMPOSIUM SPONSORED BY
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Foreword

Arthur L. Welden
Mesoamerican Ecology Institute and Department of Biology,
Tulane University, New Orleans, LA 70118

The rate of destruction of tropical forest is mind-boggling even to those of us familiar with chainsaw and bulldozer. Figures on acreage cleared each year are so high as to numb the mind. The political and economic pressures on tropical forest lands seem to be irresistible, but resisted they must be. It behooves those of us working in tropical forests to present cogent economic and political, as well as biological, reasons to halt what appears to us to be short-sighted exploitation of such a world resource.

The Mesoamerican Ecology Institute assembled five students of those forests and their people, who have been supported in their efforts by the Mesoamerican Ecology Institute, to speak on various aspects of tropical forests. We present these talks to join our voice to those of other concerned organizations. Our approach was to point out the complexity of these ecosystems, their genetic diversity, how various people, indigenous and otherwise, perceive this destruction and accommodate to it, why the forests are being destroyed, and the economic consequences of such destruction. Dr. Thien has investigated forest structure and pollination mechanisms in tropical forest of both hemispheres. He is vividly aware of the delicate balance of these ecosystems and how fragile they are. Dr. Arturo Gomez-Pompa makes the argument that the genetic diversity of tropical forests is a rich larder for mankind's betterment. As former Director General of the National Institute for the Investigation of Biotic Resources of Mexico and as a prominent member of the Mexican team that located and studied the pharmaceutically invaluable *Dioscorea* of Mexico; he is well qualified to speak on this subject.

Dr. James Nations is well-known for his studies of the Lacandon Maya and for his knowledge of forest destruction to produce food, not for local consumption but for export markets. His paper reveals forest destruction not for the benefit of what is often a malnourished local population but for the "fast-food" market in distant countries. Everyone, sooner or later, loses when complex, genetically diverse ecosystems are converted into ecologically and genetically simplified ones. The loss is amplified by several magnitudes when we realize that frequently the soon abandoned grasslands which replaced the forests prevent the return of the forests. Species, many unique and many of future economic value, have disappeared forever. The ancient rule to make changes slowly has particular pertinence when dealing with forest ecosytems.

Dr. Sullivan demonstrates how the Maya of Quintana Roo, Mexico use this rule to the extent they can under modern pressures. The flexible system used by these indigenous people to cope with modern innovations under sometimes inappropriate conditions may teach us valuable lessons in exploiting tropical forests.

Finally, Mr. Hazlewood of the World Resources Institute recapitulates the devastating effects of deforestation and emphasizes the economic impacts on agriculture, energy, forestry, and health.

Mr. Hazlewood stresses the need to increase political awareness of the problem of deforestation and spur action by a more comprehensive accounting of the economic costs of forest depletion. He further points out the effects of land use policy (open access) in accelerating deforestation. As Dr. Gomez-Pompa and Mr. Hazlewood point out, deforestation is not generally recognized as a major public policy issue. Perhaps, the economic analysis of the type proposed by Mr. Hazlewood will clarify the economic benefits of sustainable forest management and move the question into the public policy arena.

We at MEI hope that this symposium and others like it will stimulate more public awareness of the consequences of tropical deforestation. Efforts such as these may help governmental and developmental agencies to increase their efforts to preserve tropical forests.

Complexity of Tropical Rain Forests

Leonard B. Thien, Victor Rico-Gray,
Alfred E. Smalley, and Anne S. Bradburn
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Tropical forest ecosystems represent the most complex assemblages of organisms on earth. In a given community thousands of organisms interact with one another and form an intricate web of energy flow and productivity. These forests differ greatly from one locality to the next and have been assigned a variety of names such as: humid tropics, tropical evergreen alluvial forest, dry tropics, white sand forests, etc. (Walter, 1971). Botanists throughout the world now classify these forests into 30-40 types (Caulfield, 1984). The term "tropical rain forest" which was coined by Schimper (1898, 1903), is used by many biologists as a general designation of these various forests. In "The Primary Source", Myers (1984) defines tropical forests as, "forests that occur in areas that have a mean annual temperature of at least 75 degrees Fahrenheit and are essentially frost free in areas receiving 2,000 mm or more of rainfall per year and not less than 100 mm of rainfall in any month for two out of three years. They are mainly, if not entirely, evergreen. We generally find such forests at altitudes below 1,300 meters, though sometimes in Amazonia up to 1,800 meters and usually in Southeast Asia up to only 750 meters. In mature tracts of forest, there are several more-or-less distinct strata, and the canopy is made up of almost continuous interlocking tree crowns".

Apparently the first person in western society to describe tropical rain forests was Christopher Columbus in 1493 upon visiting the island Espanola (Hispaniola)—the island that is now politically divided into Haiti and the Dominican Republic (Caulfield, 1984). Subsequently European explorers of the American tropics were the sixteenth-century conquistadors (Jordan, 1982) and several centuries later the great naturalists such as Bates (1892) and Wallace (1889).

LOCATION. Tropical rain forests exist essentially as a band around the middle of the earth concentrated on land areas between the Tropic of Cancer and the Tropic of Capricorn (Rumney, 1968). *Tropos* is Greek for "turning point" referring to the sun's zenithal position in the sky. Tropical rain forests occur in three major areas: 1) In Central and South American and the West Indies, 2) In Africa, essentially in the Congo, Niger, and Zambezi river basins and Madagascar, 3) In the Indo-Malay-Borneo-New Guinea regions of Southeast Asia.

Originally approximately 12% of the earth's surface (5 billion acres) was covered with tropical vegetation (Table 1). An estimated 50% of this vegetation has been destroyed (Table 1). The Amazon valley bounded by the Guyana and Brazilian Shields (Sterling, 1973) contains the largest continuous tract of tropical rain forest in the world with about 3.6 million square kilometers (Myers, 1979). South-east Asia has the next largest concentration of tropical rain forest followed by Africa (Table 1).

TABLE 1. Area, biomass, diversity and destruction of tropical rain forests of the world. Excerpts taken from Caulfield (1985) and Myers (1984).

	Caulfield	Myers
AREA		
	Originally 12% of earth's surface (5 billion acres now 50% destroyed).	Once covered 16 million sq. km. now ca 9 million sq. km. Maximum 5.1 million sq. km. in Latin America, 2.1 million in Asia, 1.8 million in Africa, Indian Ocean and Pacific Ocean islands. 1/3 of world's forest with 4/5 of Earth's land vegetation.
BIOMASS		
	Average dry weight (biomass 180 tons/acre) (temperate deciduous forest 120 tons/acre).	1,000 tons of plant biomass/ha, dipterocarp forest of Borneo. 30,000 tons on 45 ha (760 tree sp) Brunei 165 kg fauna/ha.
DIVERSITY		
	Plants	Plants
	40-50% of world's living things. 40-80 tree species/acre; temperate deciduous forest 4 species/acre (trees). New Caledonia—3,000 species of plants; Great Britain (13.5 x larger) has 1,800 species. Madagascar—2,000 tree species; North America temperate zone, has 600 tree species. Panama has as many plant species as all of Europe. Mt. Makiliang, forested volcano in Philippines, has more species of woody plants than United States.	4,000 orchid species in S. E. Asia (1/4 of Earth's total). S. E. Asia supports 1 in 10 of all plant speies in just 3% of the planet's land surface. 2,500 tree species on 126,000 sq. km. in Brunei and Sarawak. Amazonia—30,000 plant species; 10,000 species in all temperate S. America. Brazil, 20,000 plant species, Costa Rica, 8,000 Ecuador, 15-20,000 plant species (Great Britian, 1,433 species). Peninsular Malaysia equal 0.09% of Earth's surface supportst 8,500 species of plants or 3.4% on planet. Mt. Kinabalu has 5 times as many oak species as the whole of Europe. Highest diversity—Rio Palenque (western Ecuador (1.7 sq. km.) 1,025 plant species followed by Choco regions in Colombia with 208 tree species in 1/10 ha. Next largest center in S. E. Asia.
	Animals	Animals
	16% of all bird species in world occur in Indonesia (1480 out of 9,000). Papua New Guinea—320 endemic species of birds. 300 sq. miles in Panama/Costa Rica has 500 resident species birds (4 times as many as in temperate forests of eastern U. S.). 500 insect species in 2,000 net sweeps in understory of Central America. 1 sq. m of leaf litter—50 species of ants, Central America.	Amazonia has 1 in 5 of all bird species on Earth. Peninsular Malaysia—675 bird species and 200 mammals. S. E. Asia (whole 656 mammal species, 850 amphibians and 700 butterfly species. 2,000 fish species in Amazon River and tributaries (10 times as many as in all Europe: 8 times that of Gunung Mulu Park (Sarawak)—20,000 species of invertebrates (529 sq. km.). Panama—1,200 species beetles on a single tree (*Luehea seemannii*). About 41,000 arthropods/ha in Panama.
DESTRUCTION		
	1/5 of remaining tropical forest will be destroyed or severely degraded by end of century. Individual losses: (% of remaining) Philippines 20% Indonesia 10% Nigeria 100% Madagascar 30% Costa Rica 8% Mexico 35%	Tropical forest ecosystems have been in existence for at least 50 million years. Within a period of half a century they will be eliminated. The destruction period—one-millionth part of their history.

Tree heights and stratification of the tropical rain forest vary depending upon rainfall and other environmental factors. The structure of a typical tropical rain forest is discussed by Richards (1952). In general tree heights do not exceed 50-55 meters (Walter, 1971). The trees are straight and slender; they begin to branch only just below the apex and thus crowns are small. Commonly, the trees form buttress-like roots. These plants tend to have a large number of epiphytes and lianas attached to them (Walter, 1971; Putz, 1984).

Thus viewed, a typical rain forest has the following stratification: 1) Scattered very tall emergent trees that project above the general canopy, 2) The canopy layer which forms a continuous aerial carpet, 3) One or several understory layers, 4) A seedling layer on the forest floor. As noted by Janzen (1977), the relatively uniform green color of the vegetation disguises its true nature from the prospective herbivores. Mature tropical rain forests tend to be open and park-like and easy to walk about in. The most frustrating factor about visiting a tropical rain forest is that most of the biological activity takes place in the canopy and one only catches a glimpse of the activity. In recent years special rope climbing techniques have been employed to put observers in the canopy (Perry, 1984).

In terms of aerial phytomass (wet weight) the various components of the forest are distributed as follows: leaves, 2-3%; branches and twigs, 26-30%; stems, 60-65%; other plants, (lianas, epiphytes, etc.), 5-8%. Although liana biomass generally represents < 10% of the forest biomass, up to 40% of the total leaves in the canopy may be formed by lianas (Ogawa, Yoda, Ogino and Kira, 1965). A large proportion of the living material of the forest may be located in the roots. In some forests, such as the white sand vegetation of the Amazon basin, roots comprise 60% of the total biomass, compared to other Amazon forests having only 20% (Anderson, 1981).

DIVERSITY AND DISTRIBUTION. The tropical rain forests of the world are noted for their high diversity of plants and animals. Visitors from the temperate zone are overwhelmed by the great numbers and interactions of the organisms. Popular and technical articles (Sterling, 1973; Prance, 1982; White, 1983) repeatedly discuss the diversity and distribution of plants and animals. Table 1 presents some of the more striking statistics and comparisons of diversity in tropical rain forests.

The destruction by man of tropical rain forests throughout the world in the next fifty years will result in the extinction of a great number of these plant and animal species. The estimates of the number of species that will become extinct varies greatly (400,000 to over a million) depending upon the authority (Harwood, 1982) but all seem to think it will be the greatest extinction of species in the history of life on earth (Myers, 1984). Why the discrepancy in estimates? No one knows the number of species of organisms existing on the planet. Approximately 1.5 million species of organisms have actually been described by taxonomists (Harwood, 1982). Most of the organisms already described live in areas outside of the tropical rain forests. How many species await discovery and description? Paul and Anne Ehrlich suggest between 2 and 20 million (Harwood, 1982). Myers (1984) estimates something like 3-10 million species. Peter Raven, director of the Missouri Botanical Garden, estimates 4.5 million species as the smallest possible total for the earth (Harwood,

1982). Most of the undescribed species of plants and animals live in the tropics. All of the above suggested figures may be incorrect. In a study of Coleoptera and other arthropod species in tropical forest Erwin (1982) states, "It should be noted that there are an estimated 50,000 species of tropical trees (R. Howard and R. Eyde, pers. comm.). I suggested elsewhere (Erwin and Adis, 1981) that tropical forest insect species, for the most part, are not highly vagile and have small distributions. If this is so, and using the same formula as above starting with 162 host-specific beetles/tree species then there are perhaps as many as 30,000,000 species of tropical arthropods, not 1.5 million". With the destruction of the tropical rain forest within the next fifty years a very large number of organisms will become extinct before they are even known to man.

MAN, SOILS AND AGRICULTURE. There is a great deal of controversy surrounding the fertility of soils in tropical rain forests and the ability to sustain agriculture. Can the tropical rain forest be utilized for intensive agriculture without allowing the land to lay fallow for a period of time? The slash and burn technique of agriculture has been used by man for thousands of years to grow food in the tropics. The first year's crop is very good but the subsequent crops display a dramatic decline in production. Currently large areas in the Amazon basin are being cut and burned by large multi-national corporations for cattle raising. In many cases the cut trees are not salvaged for lumber but simply burned and the land planted with a single species of grass seed (Silva, 1979). In Brazil pasture land is 85% *Panicum maximum* (Toledo and Serrao, 1981). Myers (1984) refers to this as the hamburgization of the Amazon Basin. This noninflationary beef supplies the fast food restaurants of the world, particularly in the United States. The pasture cannot be sustained after 5-7 years and then more vegetation must be cut and burned (Myers, 1984). There are reports, however, that maintain the pastureland can be sustained indefinitely if fertilized (Toledo and Morales, 1979; Sanchez, 1981).

The soils of the tropical rain forest vary in structure and fertility (Richards, 1952). The distribution of soils in the tropical rain forests of the world shows a dominance of acid, infertile soils. The smallest proportion of fertile, well drained soils occur in Latin America (Sanchez, 1981). Southeast Asia has a large percentage of fertile soils (with many "problem soils") with the soils of Africa falling between these two areas (Sanchez, 1981). Technical descriptions of tropical soils have been reported by Sanchez and Cochrane (1980) for tropical America, Dent (1980) for tropical Asia, and Moormann and Greenland (1980) for tropical Africa. The knowledge of soils of the Amazon basin is more complete than for any other tropical region of the world except peninsular Malaysia (Sanchez, 1981); Cochrane, *et al*, 1979; Cochrane and Sanchez, 1981).

The classification and nomenclature of soils is confusing. The following paragraphs briefly discuss the major soils of tropical rain forest areas using the terminology employed by FAO (Food and Agriculture Organization of the United Nations). Information in this listing was taken primarily from Sanchez (1981) and Hecht (1981).

Oxisols– low fertility but with favorable physical properties. Red or yellowish. Acid, deficient in P, K, Ca and micronutrients—often with toxic levels of Al. In the New World mainly in areas affected by the Guyana and Brazillian Shield.

Pacific Coast of Colombia. In Africa in Cameroon, Gabon, central Zaire and Madagascar. Not extensive in tropical Asia.

Ultisols– low fertility, poor physical qualities (increase of clay with depth). Red or yellow. Acid, susceptible to erosion. Predominant soils of the Amazon basin west of Manaus. Dominant on Atlantic Coast of Central American and humid coastal Brazil. Abundant in tropical Asia and Africa.

The above two soil types are not susceptible to laterite formation. These two soil types occur in 63% of the world's humid tropics. In tropical America 82% of soils are either oxisols or ultisols (56% in Africa and 38% in Asia).

Inceptisols– young soils.

aquepts– (poorly drained). In Asia these soils are devoted to rice production. Half of the aquepts soils in the Amazon basin are in varzeas; the rest are aquajales (mainly palm swamps).

andepts– (volcanic origin). Lack high phosphorus fixation capacity. Important in Philippines, Java, Sumrata and parts of Central America.

tropepts– (well drained, non-volcanic). Moderate to high fertility. Not extensive in tropical America or Africa.

Entisols– recently developed.

fluvents– along major river valleys. Common in Asia.

psamments– deep sandy, acid, low fertility. Western portion of Congo Basin, some areas of Brazil and Asia.

Alfisols– many cannot be separated from oxisols and ultisols without chemical analysis. Most are deep, well drained and red or yellow. Occur in spots surrounded by oxisols and ultisols in the Amazon Basin. Fertile. In Africa, however, they have a sandy gravelly surface underlaid by plinthite. This soil becomes acidic when fertilized and are the dominant soil of the forested zone of West Africa.

Vertisols– heavy clay soils that shrink and crack with changes in moisture. They are well supplied with nutrients except for nitrogen and phosphorus. Not abundant in tropical rain forest.

Mollisols– are highly fertile, typical of temperate grasslands, with a spotty distribution in the tropics.

The alfisols, vertisols and mollisols, plus andepts, tropepts and fluvents are the best soils of the humid tropics but account for only 221 million hectares or 15% of the area of the humid tropics (7% in tropical America but 33% in Africa).

THE COUNTERFEIT PARADISE. A review of any general ecology text will show that the natural productivity of tropical rain forests exceeds or equals that of any ecosystem on the planet (Odum, 1971; Whittaker, 1975). If the soils are poor and sustained European and North American agriculture is not possible, why is the natural forest so productive? The entire nutrient capital necessary for continued growth is tied up in the living matter itself (Walter, 1971). One way of viewing this is to compare the distribution of carbon in a typical coniferous forest versus a typical tropical rain forest (Odum, 1971). Approximately 50% of the carbon in the ecosystem of the northern coniferous forest is located in the soil versus less than 20% in the soil of the tropical rain forest. The tropical rain forest may be viewed as epiphytic upon the soil (Anderson, 1981). The concept of great fertility was supplied by early conquistadors (Jordan, 1982) as Europeans commonly equated the sizes of trees with soil fertility. However, the tropical rain forest, although very productive in the natural state, gives a false impression of fertility from man's temperate agricultural point of view; thus the term "counterfeit paradise" (Meggers, 1971) is used to express the contradiction.

Sustained agriculture does not seem to be possible in most regions of the tropics, for with removal of the vegetation the soil nutrients, low to begin with, are leached by the heavy rains to levels that cannot sustain a harvest to justify the energy input needed. How does a tropical rain forest ecosystem manage to maintain the nutrients in the living biomass? The theory that nutrients are

intercepted and taken up rapidly before they are lost from the system is called direct nutrient cycling and was put forth by Went and Stark (1968). It is direct because the nutrients move directly from decomposing organic matter to roots via mycorrhizae (Jordan, 1984) and by-pass the soil. Very few workers have tested this theory but in a study of nutrient retention in the Amazon Basin, Stark and Jordan (1978) sprayed radioactive labeled P and Ca directly on the root mat. Less than one tenth of 1% of the radioactivity applied to the study plots was recovered. One month after application no levels of radioactivity could be detected in the study plots. In this area of study (oxisol soil type) the roots occurred primarily in the humus layer, near the surface, and in some places formed a mat 10-30 cm thick on top of the mineral soil. Indeed in some areas the root mat could be peeled from the soil like a carpet (Stark and Jordan, 1978).

There are other means whereby trees in the tropical rain forest conserve and allocate minerals. In some types of tropical rain forest, such as moist subtropical montane forest, canopy lichens are a source of nitrogen (Forman, 1975). Lichens containing blue-green algae (*Nostoc*, *Gloeocapsa*) capable of fixing atmospheric nitrogen are common in Colombia. An estimated 13,600 macrolichens per hectare were found to contain *Nostoc* (biomass 5.7 k.7 kg/ha). Fixation of nitrogen by these lichens yielded an estimated 1.5-8 kg N/ha/yr. The death of lichens and steady precipitation would presumably distribute nitrogen in the ecosystem (lichens are rare in forests with a pronounced dry season).

Another means whereby trees in tropical rain forests gain access to nutrients has recently been elucidated. In the montane cloud forest of Costa Rica, twenty-two species of trees have been found with canopy roots (Nadkarni, 1981). Epiphytes (particularly bromeliads) are common in the tropical rain forest and have been considered by some workers to be "nutrient pirates". The roots and leaves of many epiphytes accumulate organic material (fallen leaves, tissue produced by the growth of the epiphyte, etc.). The host trees in some instances put forth adventitious roots that run beneath these mats of accumulated organic matter and utilize the minerals (Nadkarni, 1981).

Although the root mat of the tropical rain forest is very good at capturing minerals there is leakage from the ecosystem. An important source of minerals to replace the leakage, particularly in the Amazon Basin, is precipitation (Jordan, 1982). In an area at Rio Negro (Jordan, 1982) which receives 3,500 mm annual rainfall (with no month receiving less than 100 mm), nutrient input via precipitation was measured over a two year period. It was concluded that input of minerals via rainfall exceeded loss of minerals via leaching (raining fertilizer). Therefore weathering of rock really is not contributing to the nutrient economy of the forest.

CONSEQUENCES OF DESTRUCTION. The climax tropical rain forests of the world are being destroyed at a tremendous rate (Table 1). The slash and burn method of agriculture is being abandoned in large areas in favor of cattle ranching, or forest is simply totally cut to make composite wood (De'Ath, 1980). Man has been utilizing the tropical rain forest for a long time. The oldest evidence of human presence in the interior Amazon Basin for example is 3,750 years B. P. + 20 (Sanford, Saldarriaga, Clark, Uhl and Herrera, 1985).

In the method of slash and burn agriculture, small areas of forest are cut, allowed to dry and are then burned. After growing crops for one to two years, the plot is abandoned and allowed to revert again to forest. Thus plant succession is allowed to repair the damage to the original forest. In the succession process, seeds that remained in the soil germinate (Ewel, Berish, Brown, Price and Raich, 1981), and stump sprouting may occur if the fire was not too intense; seeds of primary tree species are brought in by animals (Foster and Brokaw, 1982). Actually, disturbance of vegetation, especially by fire, appear to have played major roles in the history of tropical rain forest vegetation. Earthquakes occasionally denude large areas of tropical forest especially in mountainous areas such as New Guinea and Central America (Garwood, Janos and Brokaw, 1979). Recent evidence indicates that charcoal is common in the soils of mature rain forest in the north central Amazon Basin. The fires which formed the charcoal may have been common for the past 6,000 years (Sanford, *et al*, 1985). Treefalls in mature tropical rain forests occur often enough (one per hectare every 5.3 years) and create large gaps over 150 sq m to allow pioneer trees to colonize (Brokaw, 1982). Also aridity in the Pleistocene has apparently affected the evolution of tropical rain forest. Ten thousand years ago, in the Peten in Guatemala, vegetation consisted of marsh, savanna and juniper scrub (Leyden, 1984). Thus the rain forests of Guatemala are no older than 10,000–11,000 years (Leyden, 1984).

The point is that tropical rain forests have been disturbed for thousands of years and plant succession has been a factor in the repair process. Slash and burn agriculture has been successful for man because it imitates the natural disturbances of the forest. However, what is going to happen to the forest and the people now that large areas are being cut and losing contact with uncut regions?

Gomez-Pompa and Vazquez-Yanes (1972) suggested that the primary trees of the tropical rain forest would be incapable of regenerating under present land-use strategies. The primary trees originate from neighboring uncut areas. As large expanses of land are utilized the sources of seeds become smaller and the numbers of dispersal agents also diminish. After a period of time only secondary species are capable of surviving. These species are generally lower in stature and the biomass lower. Indeed there may already be areas in the world where only secondary vegetation can occur. As a result there is a great loss in diversity and gradual erosion of the ecosystem. Recent work on ecosystem decay (Lovejoy, Rankin, Bierregaard, Brown, Emmons, and Van der Voort, 1984) suggest that the above theory is correct.

In wet tropical rain forest there are two main groups of seeds according to their germination behavior. One group comprises seeds (canopy species) which germinate in stable conditions on the forest floor. The trend is for rapid formation of partially or totally dormant seedlings that are less susceptible to predators (Vazquez-Yanes and Segovia, 1984). The second group of seeds has delayed germination adapted for establishment in gaps and other disturbances (secondary species; Vazquez-Yanes and Segovia, 1984). With the cutting of large areas of tropical rain forest, rainfall patterns may be greatly altered. It has long been observed in tropical areas of the world that the cutting of vegetation seems to decrease rainfall. Another con-

sequence of destroying the vegetation is an increase in water runoff from the land followed by erosion. For example, the Amazon River has a discharge (5.5 N 10 m yr) five times that of the Congo and represents 15-20% of the *global* freshwater supply (Salati and Vose, 1984). In the Amazon Basin about 50% of the rainfall is evapotranspired as water vapor back into the atmosphere, of which 48% falls again as rain. This represents a recycling rate of about 5.5 days. Detailed studies at Manaus (2,000 mm/yr) indicate a much higher evapotranspiration rate. In one study 18.7% of rainfall was intercepted by the forest and evaporated back, 62% was transpired and 19.3% was runoff; in another study the figures were 25.6%, 48.5% and 25.9% respectively (Salati and Vose, 1984). The implication is that large-scale deforestation, if continued at current rates, must inevitably affect the present equilibrium of the water cycle (Salati and Vose, 1984). The effects could be continental or global. As noted earlier the tropical rain forests in Africa occupy the smallest area of the three areas of concentration. Compared with rain forests on other continents, the African tropical rain forest is relatively dry and receives between 1600 to 2000 mm rainfall per year (distribution is also uneven; Tucker, Townshend and Goff, 1985). The areas receiving more than 3,000 mm per year are largely confined to the coast. Analysis of the African rain forest throughout the year using satellite data dramatically displays the large areas that are affected by seasonal dry patterns. If rainfall is indeed reduced by cutting of the forest, fire may begin to play a major role and desertification processes set in motion.

INTERACTIONS–MOSTLY INSECTS. Tropical rain forests are not only structurally and physiologically very complex but the interactions organisms are perhaps even more complex. As Myers (1984) states, "After all, if there are 1,000 species within one particular square kilometer of forest, their relationships with each other—their comings and goings, their incessant encounters with associates and enemies—certainly number tens of thousands of interactions, probably hundreds of thousands, possibly many more". Ecological interactions have long been recognized as important factors influencing the evolution of species, but few explicit models of the evolution of these interactions exist. One possible way of explaining this lack of information is that the interactions are more ephemeral and less tangible than species, but certainly must be the result of evolution (Thompson, 1982; Futuyma and Slatkin, 1983). It is important, in terms of evolutionary ecology, to study the origin of interactions (Thompson, 1982) and their patterns.

Gilbert (1980) suggests that patterns of chemical defenses (and of insect feeding) are generated by a process of coevolution between plants and their parasites. He coined the terms "mobile links" and "keystone mutualists" to describe interactions between certain key organisms in tropical rain forests (Gilbert, 1980). Animals (as Euglossine bees) that are major factors in the presistence of certain plant species which also support separate food webs are called mobile links. Keystone mutualists are those organisms which provide support to large complexes of mobile lines (many are successional species of plants, as species of *Heliconia* and members of the Solanaceae).

The various kinds of interactions can be divided roughly into negative or antagonistic, and mutualistic (Thompson, 1982). Antagonistic in-

teractions occur between species because living organisms are concentrated packages of energy and nutrients and because resources are limited (competition; Thompson, 1982). The most common categories of these interactions are parasitism, grazing, and predation. Competition differs greatly from other kinds of interactions because species that initially have similar use of a resource diverge in time (Thompson, 1982). This makes competition generally less likely to lead to long-term coevolution of sets of species than other forms of antagonistic or mutualistic interaction (Thompson, 1982).

In mutualistic interactions associated members receive some sort of benefit which enhances their general fitness. Mutualisms seem to be more common in tropical areas, particularly in regard to pollination systems, seed dispersal and extrafloral nectary systems. However, species richness, biomass, diversity, and productivity also increase in the tropical rain forest and there must be an increase in the number of interactions.

A good example of the change of interactions from antagonistic to mutualistic is the interaction between plants and the animals that pollinate them. The habit of feeding on spores is very old for terrestrial arthropods (Malyshey, 1968, in Strong *et al*, 1984) and apparently early insects pollinating angiosperms fed on pollen, ovules, etc; undoubtedly the vast majority of these interactions provided a basis for natural selection. The transition from antagonism to mutualism, favoring pollination by insects over pollination by wind may have been a consequence of changing climates selecting against wind-pollination. Benefits of insect pollination may have outweighted pollen and ovule loss and conferred a net energy gain compared to decreasing efficiency from wind pollination (Raven, 1977; Thompson, 1982). Furthermore, the development of floral nectaries reduced the cost of interaction relative to the gain.

As noted in Table 1 ants are abundant in tropical rain forest. Spectacular mutualistic interactions have been described in which ants act as protective agents of plants against herbivores and competing plants (Dirzo, 1984; Janzen, 1966). Ants interact widely with a variety of other life forms, doing or performing such activities as seed harvesting, leaf cutting, tending ant-gardens, or pollinating. These interactions between plants and ants have been classified in different ways using a variety of categories (Huxley, 1978; Buckley, 1982; Schemske, 1983).

An example of mutualistic interaction between ants and a plant is given below, in which the ants receive domantia and food; presumably the plant receives an increase in fitness.

Schomburgkia tibicinis (Orchidaceae) occurs throughout Central America in a variety of habitats (Jones, 1965). The plants are most often found growing high in large trees throughout tropical regions of Central America making observation difficult; however, a unique shrub community with a maximum height of 2 m on the Yucatan Peninsula, offers easy access to large numbers of *S. tibicinis*. This area, called a matorral by Miranda (1958), stretches across the northern coast astride a series of old parallel beachheads and is bracketed by sand beach and mangrove swamp or mixed tropical deciduous forest. The interactions occurring between the ants and plants on the matorral are assumed to be similar to those in wetter habitats throughout Central America.

Although a few plants can be found in anthesis throughout the year, the peak flowering period of *S. tibicinis* occurs from the middle of the dry season to the beginning of the wet season (April-June). Orchid clumps may be readily spotted from great distances as their flowering peduncles rise 1.5 to 2 m above the tops of the shrubs (ca 138 clumps per ha).

The plants of *S. tibicinis* have large, hollow pseudobulbs (to ca 4 cm in diameter and 40 cm long) with a coin-like slot at the base that are inhabitated by ants. A wide variety of animals may also live among or in old and new pseudobulbs, including snakes (boas are common), mole crickets, millipedes, and bees. Thirteen species of ants live in the hollow pseudobulbs, in old inflorescence spikes or in the soil directly beneath the plants. The ant species are as follows: *Azteca* sp, *Brachmyrmex* sp, *Camponotus* (*Myrmobrachys*) *planatus* Roger, *Camponotus* (*Myromcladoecus*) *rectangularis* Emery, *Camponotus* (*Myrmothrix*) *abdominalis* Fabricius, *Crematogaster* (*Orthocreama*) *brevispinosa* Mayr., *Ectatomma tuberculatum* (Oliver.), *Monomorium* (*Carbonarium*) *ebeninum* Forel, *Paratrechina longicornis* (Latreille), *Pseudomyrmex* sp A, *Pseudomyrmex* sp B, *Pheidole* sp, *Zacryptocerus* (*Harnedia*) *maculatus* (Fr. Smith). Although in most cases several species of ants occupy the same plant, strong territoriality separates the species; two species of ants never occur or nest in the same pseudobulb. Only six species of ants utilize the inflorescences of the plant: *Camponotus rectangularis, Camponotus planatus, Crematogaster brevispinosa, Ectatomma tuberculatum, Pseudomyrmex* sp, and *Pheiodole* sp. All these ants take nectar from developing peduncles, floral buds and parts of the mature fruit. If the ants are removed from the inflorescences, nectar drips from these various plant structures. However, only one species of ant occupies a given peduncle of inflorescence. The same species will dominate all such structures produced by a given orchid plant (clump).

One species, *Crematogaster brevispinosa*, herds the common citrus mealybug, *Plannococcus citri,* and perhaps other species, on the developing peduncles of *S. tibicinis*. Of the plants dominated by *C. brevispinosa*, 80% have mealybugs on some of their peduncles. The ants guide or carry the mealybugs to the apical meristem of the peduncle and the mealybugs feed by inserting the proboscis into the sieve cells of the outer layer of tissue. The ants take the honeydew from the anus of the mealybugs. As the peduncle grows (rate of ca 1 cm/day) the tissue becomes woody and the ants then move the mealybugs to the tip. Upon molting, the mealybugs leave their exoskeletons with proboscis inserted into the peduncle and the liquid that exudes is also harvested by *C. brevispinosa* until all the stalk tissue becomes woody and dripping ceases.

It is obvious what the ants receive from this relationship, but do the plants receive any benefit? Observations suggest the ants drive off herbivorus insects that feed on the peduncles, flowers and fruits of the orchid. The fruit and flowers of plants without ants are usually partially or wholly eaten. Perhaps the ants increase the reproductive fitness of the plants and the plants derive nutrients from material carried by ants into pseudobulbs.

Undoubtedly there are thousands (or ten or hundred of thousands) of mutualistic interactions taking place in the tropical rain forest, involving not only ants but many other types of insects. An example of ants protecting sa-

plings from herbivores was only recently elucidated. Koptur (1984) determined that *Inga densiflora* and *Inga punctata* have foliar nectaries that are visited by a variety of ants. Extrafloral nectar secretion on new leaves is continuous throughout the day and night; ant activity on both old and new leaves is also continous. Experiments were performed to compare the effectiveness of the five ant species in removing caterpillars and other insects from the leaves. All ant species tested could remove herbivores, but *Pheidole biconstricta* was the most effective. Leaves from saplings with ants excluded suffered substantially greater damage than control leaves.

Interactions of saplings and insects in tree gaps appear to be important in determing the structure and function of tropical rain forests. The evolution of different antiherbivore systems may depend on the risk of discovery by herbivores (escape). In a study of herbivory on Barro Colorado Island, Panama, Coley (1983) showed that saplings of the pioneer and permanent trees in the gap are equally easy for insects to locate. She suggests specialized herbivores and not escape is the major factor in herbivory. Apparently pioneer species are simply able to tolerate high rate of herbivory because of cheaper leaves and faster growth rates (Coley, 1983). Habitat quality is suggested as a major selective force behind the evolution of different defensive systems. A high quality habitat is one in which rapid growth is possible. Thus in low-quality habitats the vast majority of plants would have defensive systems (chemicals, leaf fibers, etc.) whereas a mixture of defensive and non-defensive systems would prevail in a high quality habitat (Coley, 1983).

As noted by Gomez-Pompa and Vazquez-Yanes (1972), any isolated tree from a temperate forest has a greater probability of survival than an isolated tree from a tropical rain forest (primary species); this is due to the complex and delicate net of relationships of each individual with the environment.

THE FUTURE. The success of the 300,000 species of angiosperms has been largely attributed to the evolution of the mutualistic interactions of insect pollination (Burger, 1981). The future for thousands of organisms in the tropical rain forests of the world is dim. A great deal is at stake, for if these species are lost, so is the chance for discovery of new drugs. Furthermore, we may see a change in the climate of the world and collapse of the human population.

Good insight into what will be lost if large portions of the tropical rain forest are not preserved is offered by the example of the plants preserved in the Rio Palenque research station on the western coast of Ecuador (Dodson and Gentry, 1978). The entire tropical rain forest on the western coast of Ecuador has been converted by man into plantations. All that remains is 1.7 km. However, this area supports 1,025 plant species, the highest recorded concentration of plant diversity on Earth (Myers, 1984). One of these plants in the small reserve, which is gradually being undermined by the local people who are illegally cutting fire wood, is a relative of the cultivated avocado which, by supplying a rot-resistant root stock, could offer commercial benefit to avocado growers in many parts of the world. Another species of plant is a relative of cocoa which reputedly yields a tastier form of chocolate. Yet another species is a fast-growing tree (endemic to the station) which used to be the tree most favored by timber harvesters in the region (Myers, 1984). Approximately 20% of the plant species occurring at Rio Palen-

que are endemic to the station (Dodson and Gentry, 1978). The loss of vast areas of tropical rain forests throughout the world would clearly be a decline in the stability and quality of life for man. As Prance and Elias (1977) so well stated "Extinction is Forever".

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Tropical Deforestation and Maya Silviculture: An Ecological Paradox

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My main interest in the past years has been the study of the vegetation and flora of tropical Mexico. My studies as well as the studies of my colleagues and students in many different regions of the country show that there is a great diversity of vegetation types and a complex flora throughout the area of our interest.

The complexity of the vegetation and the limited knowledge of the flora available to identify the species, influenced me to concentrate my interest on one state of Mexico, Veracruz, that has a great diversity of environments and a rich flora (Gómez-Pompa, 1973).

Very early in my studies I learned that humans have great influence on the variation and distribution of the vegetation and that species distributions were strongly influenced by their actions. This fact reinforced my decision to study the successional process in the tropical lowland areas of Veracruz as a means of obtaining information that would explain the vegetation patterns that we were finding all over the humid lowlands. Most of the results of the studies of our research group in rain forest regeneration have been published or are in the process (Gómez-Pompa, Vazquez et al. 1976; Gómez-Pompa & del Amo 1985).

The project for the study of the Flora of Veracruz is well underway and the most innovative contribution has been the creation of a floristic data base and an information system that can be permanently updated and used in all our botanical studies in Veracruz (Gómez-Pompa, Moreno et al. 1985).

In our travels all over the tropics of Mexico we became more and more aware of the widespread deforestation process and the speed with which it is occurring. Even the forest reserve of Los Tuxtlas Biological Station of UNAM (National Autonomous University of Mexico), which was our main experimental area, was not exempted and more than 20% of the forest was cut by landless farmers. We also became aware that this deforestation process was occurring not only in Mexico but in other countries as well.

The objective of this paper is to present some reflections about tropical deforestation in Mexico in the light of some studies in Veracruz and the more recent ones I have been carrying on with my colleagues at INIREB-Yucatán (Sosa et al. 1985).

TROPICAL DEFORESTATION. In the academic and professional media there is no doubt of the important role that tropical forests play in the protection of natural renewable resources: water, soil, flora and fauna. Many papers have been written on the subject and meetings at a high scientific level have provided us with the basic arguments of this important function of forest resources.

In spite of the seriousness of the arguments, the present loss of forests and forest resources is alarming, especially in most tropical countries, where a high rate of deforestation is occurring (Au-

breville, 1947; Farnworth & Golley 1974; Gómez-Pompa et al. 1976; Goodland & Irwin 1975; Lanly, 1983; Whitmore, 1984). The problem becomes even greater because of the lack of sufficient programs on reforestation that could replace, in a reasonable time, the resources that have been lost.

As scientists working in the tropics we have no doubt about the important role that forests play in nature and its beneficial effects for mankind. This perception of forest values is an incontrovertible fact. The respect and admiration for trees and forests that humans have, whether belonging to an urban, industrial, or rural society are certainly linked to the thousands of years of evolution of the human brain. Our ancestors lived in or near the forests and depended on them, as they provided a good portion of their subsistence resources. The forests, and especially the rain forests, were also places of respect since some of their "enemies" (large predators and "poisonous" animals) lived and were hidden in them. This surely explains the different feeling we have in front of a tree or a rain forest than the one we have toward a grass or a savanna. This feeling toward trees and forests is a good example of *biophilia* (Wilson, 1984) and helps explain our feeling of need, appreciation and respect for nature, parks and forests as the maximum expression of places for relaxation and recreation.

The importance that modern society gives to the protection of these sites is due more to psychological reasons than to practical ones since we do not depend on these locations for subsistence.

On the other hand many traditional societies that depend on forest lands for survival have a very different perception of forests, their management, and conservation. They treat the forests with great respect (Gómez-Pompa, 1985a). The Maya for example used to ask permission of their gods for felling the forests for their milpa agriculture. For the Tsembaga in New Guinea, the forests are a worship motif (Rappaport, 1972). These attitudes become understandable if we realize that these societies depend on the forests and forest soils to obtain many of their basic needs.

The different perception of the forest and its resources by these two cultural groups (modern vs traditional) is the cause of strong contradictions (i.e., recreation vs subsistence), in spite of having the same atavistic roots.

The protection and the use of the rain forests mean two entirely different things for a subsistencce farmer who lives in and from the forest, and for an urban person who only knows the rain forest from a photograph or from watching TV. The first has to make decisions on a daily basis for the future of his resources, so whatever he does is conditioned by forest survival. The second one often has to make decisions that will affect the rainforest regions without his being aware of it. The most important decisions for the future of these areas and their inhabitants are made by members of the dominant urban society; a society which, paradoxically, is also the promoter of parks and nature conservation.

Agricultural and forest production of the tropical forests is also perceived in a completely different manner by the subsistence farmer mentioned before than by a commercial farmer. The subsistence farmer bases his actions on successful traditional experience to insure forest survival in the area. The latter sees the forests and soils only as a source of cash. The first one has a peasant economy strongly based on his survival

which is linked to environmental conservation and less oriented to trade and market. The second one is basically oriented to the market as a way of survival.

This difference in perception in relation to the protection and production of the forest regions is one of the main causes of deforestation in the tropics and is the one to which I will refer in this paper.

I don't think it necessary to make another general review of what is already known of the problem of tropical deforestation. Many workshops and papers have been dedicated to this subject (FAO, 1981; Myers, 1980; Tucker & Richards, 1983; UNESCO et al., 1978; USSD, 1978). In spite of the lack of agreement on the rates of deforestation and the urgency of the problem, it is openly acknowledged that tropical deforestation is a current trend for the tropics that should be better understood, and in several regions and countries has become critical.

On the other hand, we all know of the great difficulties of doing good tropical silviculture and forestry and how complicated it is to develop programs on silviculture and reforestation on a long term basis in the tropics (Baur, 1968; Dawkins, 1958; Mergen, 1981).

This coincidence between a weak tropical silviculture together with vast deforestation, has produced the present critical situation in many tropical countries.

The urgency for trying to find a general solution to this problem is evident. In order to understand the problem it seems necessary to make some analysis of various local situations and perhaps from them, become able to define the general problem and then try to find some solutions.

DEFORESTATION OF THE MEXICAN TROPICAL LOWLANDS. I will use some examples from Mexico to analyze the problem and with it illustrate one approach I can suggest for the solution of the acute problem of deforestation of the tropical Maya area.

Obviously, the first thing we must do is to define the problem of deforestation. Is it a real problem? Because if it is not, there is no need to be worried about it; but if it is, it is necessary to explain for whom. Also, it will be necessary to identify the persons affected by the problem and to analyze the consequences of not taking action. It will also be essential to identify those involved with the problem and to try to understand their reasons.

The problem of deforestation of the Mexican tropics has two components: the reason why it is deforested and the reason why it is not reforested. We must try to understand these aspects so we can suggest feasible solutions.

The forests of the lowland tropics of Mexico and Central America are subjected to an intensive deforestation process. There are not reliable figures on the rate of deforestation, and maybe we will never have them, because the two processes, reforestation (natural as well as artificial) and deforestation are very dynamic.

In Mexico the forests are cut mainly to use their soils for agriculture. This is done through two main processes; by governmental programs of directed colonization and by spontaneous colonization by individual actions (Gómez-Pompa et al., 1976; Halffter, 1983).

DIRECTED COLONIZATION. In the case of programs of directed colonization (Table 1) the first step is to cut the valuable timbers (which we know include only a few species) and obtain the benefits of their market value (by the

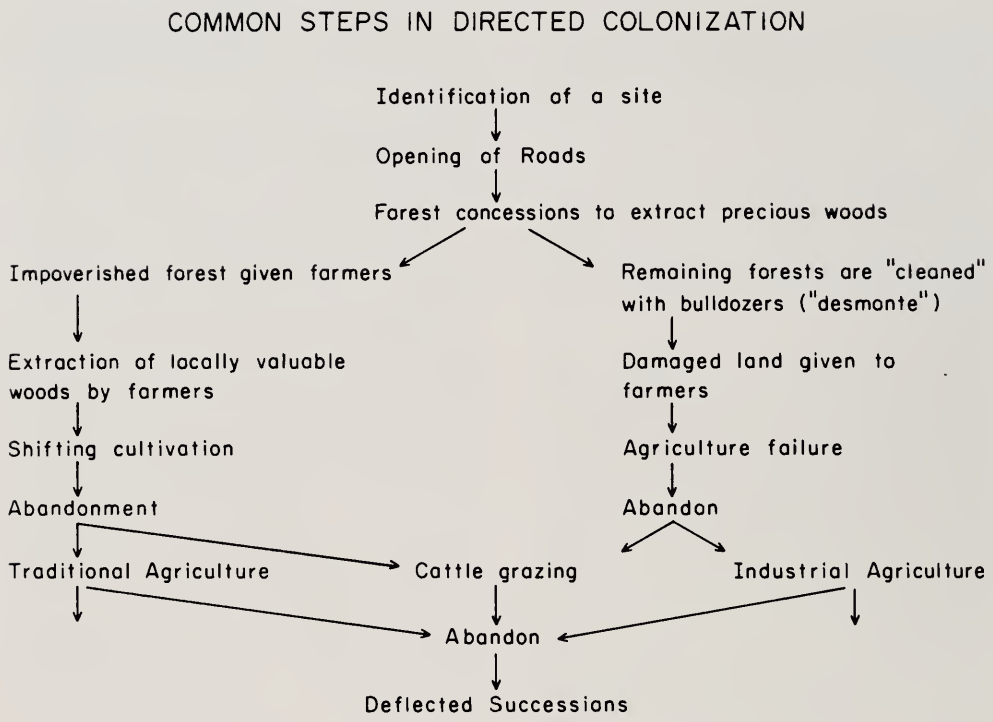

TABLE 1. Common steps in Directed Colonization Programs.

concessionaires of the cutting or "desmonte" as the process is known in Spanish). Once the "precious" woods are taken from the area, the remaining forests are completely removed by bulldozers and the land given to the farmers who will be the "beneficiaries" of the colonization program. The next step is more varied depending on the purpose of the colonization program, the degree of deforestation and knowledge of the farmers. In the Maya area the most frequent step is the use of the land with a sort of shifting agricultural technique and after some years of grazing (Fig. 1). These areas are very seldom dedicated to an intensive permanent agriculture or silviculture. Frequently these areas are abandoned and an interrupted succession occurs ("bush or grass fallow", sensu Denevan, 1981) instead of the common forest fallow of swidden agriculture.

Directed colonization is always financed by large investments (generally from the Federal Government). The participation of local farmers is minimal and mainly as paid hand labor to help in the different processes of clearing, transportation of wood, etc. And occasionally, if the farmer is a beneficiary of the colonization program, as receptor of credits for starting agricultural activities in the area.

In the tropical areas of Mexico, with a few exceptions, the process of forest exploitation is very similar to the one mentioned before. The economic resources are also external to the area and the farmer participation is also as hand labor. Once the valuable wood resources have been extracted, the area is aban-

Fig. 1. Cattle ranching is the most important activity in lowland areas in tropics and the ultimate cause of deforestation in the Maya area.

doned and shifting agriculturalists take over the site for a few years. Often the abandoned fallows are converted to grazing land.

It is a well known fact that in the Mexican tropics we have never had long term projects of forest exploitation. Regeneration is never included in the management plans. The same applies to commercial forest plantations. There are almost none in the lowland tropics of Mexico (except a pine plantation in a savannah region of Oaxaca). The well known techniques for forest regeneration and silviculture are never followed, and are used only on a small experimental scale in research stations, as happens in other tropical countries as well (Budowski, 1981).

The results of all these facts are well known; forest regeneration does not occur in these forest exploitation and colonization sites. Instead, a secondary savanoid forest takes its place, which is suitable for shifting agriculture. In areas with an abundance of landless farmers (most of the Mexican tropics) this is precisely what occurs, with the additional problem that this occupation often is illegal and the farmers, well aware of that, do not plan on a medium or long term basis.

The rest of the story is well known; many of these areas eventually are turned into areas for grazing, forcing the landless farmer to move into other areas of forest exploitation and start another cycle.

This intense process of conversion of forest systems into agroecosystems is very well known and understood not only for Mexico but for many other tropical countries as well.

SPONTANEOUS COLONIZATION. The process of spontaneous colonization (Table 2) of the forests is more difficult to describe for there are multiple factors that promote it and the proces-

COMMON STEPS IN SPONTANEOUS COLONIZATION

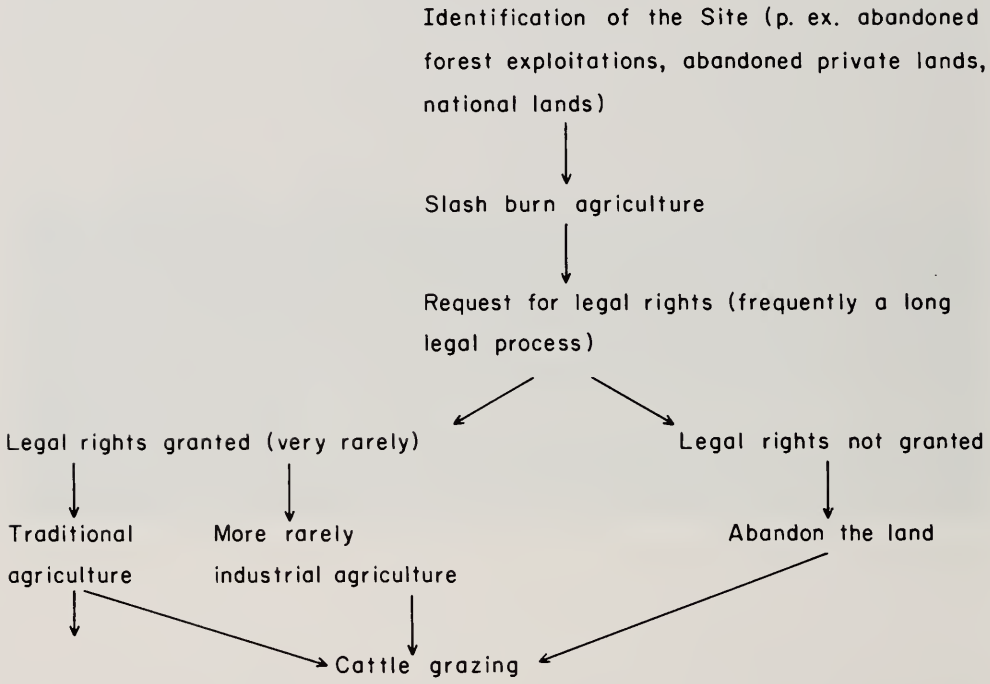
Identification of the Site (p. ex. abandoned forest exploitations, abandoned private lands, national lands)
Slash burn agriculture
Request for legal rights (frequently a long legal process)
Legal rights granted (very rarely)
Legal rights not granted
Traditional agriculture
More rarely industrial agriculture
Abandon the land
Cattle grazing

TABLE 2. Common steps in Spontaneous Colonization.

ses that can distinguish it are quite different. The most frequent means of this type of colonization is through the establishment of the "milpa" system of shifting cultivation (Fig. 2). The "milpa" techniques are the basic (and frequently the only) technology of subsistence farmers in the tropics of the world. Under conditions of isolation and low population density they form an excellent agro-forestry system. The system is well known, and several studies indicate that this system is the one best adapted to the ecological and economic conditions of the tropics (Denevan, 1981; Greenland, 1975; Hernández X., 1959; UNESCO, 1983).

When the farmers settle permanently in an area, the "milpa" system is rationalized (Fig. 3) and the farmers look for the most adequate cycles for diminishing the pests and weeds and for the recovering of fertility. In this case the "milpa" system is often complemented with other farming systems creating an ecological mosaic of land uses. This may evolve into a land use management system based on the ecological mosaic of uses and resources. The Maya, for example, included managed successions, utilization of a great variety of plants and animals from their natural and managed ecosystems, forest plantations, a diverse variety of farming systems, and conservation of semi-managed natural forest areas (Gómez-Pompa et al. 1984, Gómez-Pompa, 1987).

Unfortunately the people who settle in abandoned areas of forest exploita-

Fig. 2. Shifting agriculture is the most important farming system in the tropical world since ancient times and the principal cause of temporal deforestation.

Fig. 3. The dooryard forest gardens of the Maya provide the clues to explain the abundance of useful tree species in the "natural" rainforests. They are empirical experiments in agroforestry designs.

TWO TYPES OF SHIFTING AGRICULTURE

With legal rights to the land	Without legal rights
Careful burning	Careless burning
Perennial crops planted	No perennial crops
Careful soil selection	No selection of soil
Search for optimal fallow	Disregard for the fallow
Protection of useful trees	No protection
Medium to long term planning	Short term planning

TABLE 3. Two types of shifting cultivators.

tion are "illegal" and their permanence is not secure. For that reason their activities do not include systems that will assure regeneration and conservation of the resources for the long term. Frequently the care for the milpa and for the surrounding forests is not the same as that of those who are assured of permanency in one place (Table 3). Often these spontaneous farmers are those responsible for burning large extensions of forest areas in the tropical lowlands of Mexico. This is opposed to the rational activities and excellent use of the milpa by many other farmers with stability on their land; an outstanding example is the case of the milpa of the Lacandone Maya (Nations & Nigh, 1978).

These are also some of the reasons for which "milpa" agriculture has been blamed for deforestation of the tropics, but in error. It would be equivalent to blaming the axes and bulldozers for the deforestation process. Shifting cultivators have survived since remote times and by trial and error have developed a great diversity of techniques, including permanent agriculture.

Clearly, the deforestation process is complex and requires detailed analysis of each situation.

However, in spite of all the preceding, there is a question which has not been discussed sufficiently, in spite of its importance. It concerns whether deforestation is really a problem and for whom.

THE DIFFERENT PERCEPTIONS OF DEFORESTATION. In spite of what is generally believed, shifting agriculture practiced by expert farmers in flat soils or with moderate slopes is not the cause of considerable erosion. Even in pronounced slopes in humid climates, erosion is minimal due to the short time in which the soil is exposed without plant cover (Sánchez, 1976).

The erosion of soils in areas of low scale forest exploitation in tropical regions with slight slopes also is not a problem, at least on a short term basis; except in cases in which heavy machines are used on a large scale. In a study made at IITA (International Institute of Tropical Agriculture in Ibadan, Nigeria) it was found that the erosion produced by using native Nigerian systems for felling the forest is nearly nonexistent compared to that produced by bulldozers (Table 4).

LAND CLEARING METHOD	EROSION LOSS (TONS/HA)
Traditional slash and burn	0.01
Bulldozer with shear blade	3.82
Bulldozer with tree pusher and root rake	19.57

TABLE 4. Effects of alternative land-clearing practices on soil erosion in an Alfisol from Nigeria (Source: Annual Report from IITA, 1980).

Neither deforestation due to forest exploitation nor opening of new areas for agriculture and grazing (which is the same) represent a critical problem in the short term for farmers; on the contrary, they allow landless farmers to have new areas for growing crops and also create some temporary jobs in the clearing and extraction of wood. The same happens to small and large land owners with the additional advantage that they may obtain an additional economic reward as payment from the wood concessionaires as rights for the exploitation ("derechos de monte").

All of these short term economic effects have contributed to the belief that tropical forests are useless, and that they are waiting to be incorporated in the development of the countries.

Deforestation in the Mexican tropics also is not a serious problem for local or central governments. On the other hand, it is a short term solution to the demand for jobs and land by the farmers. Clearing and exploitation of the forests are sources of large incomes due to taxes and, for some government officials, are a source of illicit income.

Deforestation also is not a problem for the private sector since even those more closely related to the problem, who may be the forest products entrepreneurs, have their investments (saw mills, etc.) assured by the return of the invested capital. Tropical forest products business is seen as a mining business and not as a renewable resource business. Investments are very low and returns quite high.

From this analysis you can see clearly the basis of the problem of deforestation in the tropics of Mexico. In the minds of the principal decision makers (landowners, business people, cattle ranchers, industrialists) the problem does not exist.

Deforestation in the tropics has been identified only by scientists of different biological disciplines, and by groups of citizens, mainly from industrial countries, concerned over environmental problems.

The only unquestionably important scientific argument that these groups propose is that the forests and other tropical ecosystems comprise a very important reservoir of species and genes, that form the most important biological bank of mankind (National Research Council, 1980; Soulé & Wilcox, 1980). It is also a fact that modern science knows very little about these species and there are still many of them to be discovered.

Unfortunately many of the arguments that have been used to stop the deforestation process have not been based on this important argument and other, more controversial arguments, have been used. This caused attention to be diverted toward other possible effects of deforestation such as the loss of soils by erosion, the low fertility of many tropical forest soils, the possible effects of tropical deforestation in the climatic patterns of the earth, and others of less importance.

The problem with diverting attention to these other arguments is that each of them requires a different explanation and frequently the arguments have not been convincing enough (Ewel, 1981; Lugo & Brown, 1981; Sánchez & Buol, 1975). This open discussion on controversial subjects is causing more problems, since decision makers have additional arguments for not acting.

If we accept this as true, then we must concentrate our efforts on looking for solutions to the only problem that is widely recognized; the genetic erosion produced by the loss of species and of biotypes (Soulé & Wilcox, 1980; Vovides & Gómez-Pompa, 1977).

If we admit that this is a worldwide priority problem (IUCN, 1980), the solutions are very obvious and easy to identify. Among them we can mention the following.

1. Required is an efficient system of conservation of biological diversity through a network of protected areas representative of the different regional ecosystems.
2. Required also are more biologically diversified agriculture and silviculture systems.
3. There is need for better directed activity in conservation ex-situ of some valuable species for the future.
4. Those production systems that use biological diversity as a basic strategy should be stimulated.
5. It is necessary to have a more aggressive worldwide campaign using only serious scientific arguments to inform and educate people of the importance of conserving the biotic patrimony of mankind.
6. The cost of conservation should be paid by all who benefit from it; i.e., all mankind, not only those who live in the area to be conserved.

To execute these solutions implies a profound change in the point of view that prevails now relative to the management and conservation of renewable resources of the tropics.

FORESTS AND SOIL EROSION. Loss of soil by deforestation and overgrazing has been mentioned as a critical problem especially on the slopes of tropical mountains and in arid and semiarid areas.

The same type of analysis could be made to understand the "problem" of soil erosion and water loss caused by deforestation. Many papers have been written on the importance of forest lands, on the protection of watersheds, and as measures to prevent the siltation of water bodies. In this case arguments related to the conservation of biological diversity have been used in favor of protecting the forests, instead of using the

proper arguments on soil erosion and water flow.

I will use a concrete case in the center of the State of Veracruz in Mexico that may help in understanding the problem and in finding feasible solutions.

According to the studies done in this region (Koterba & Olivieri, 1983), there are serious problems of erosion, mainly on the semiarid higher slopes (above 2500 m.) of the Cofre de Perote.

Studies on the erosion of the region give us amounts up to 1295 tons per Ha per year of soil loss and an average for the whole area of 40 tons per Ha per year (Raa & Espinoza, 1983). Erosion in this area is caused by deforestation and inadequate agricultural and grazing activities. These figures indicate clearly to us that there is a serious problem. Now, who is affected by the problem?

Those who cut the pine trees for opening new agricultural fields do not see the immediate problem since they sell the wood and have their crops. Those who cut the trees receive the profits from selling the wood. The poor farmers in the area find an important income (sometimes their only income) in doing this illegal cutting and selling of wood.

The farmers are in favor of deforestation for they have new soils to cultivate or a site to take their animals to graze. Erosion is not identified by them as a serious problem, at least for the short term, since they can use fertilizers for some of their most important cash crops and if the soil is lost, they can move to another site or emigrate to a different region.

The siltation of lakes, rivers and lagoons at lower altitudes caused by erosion is not identified as a problem by those supposedly affected—as are the inhabitants of the banks of rivers or lagoons—by this influx of sediments. On the contrary some even acknowledge the importance of the sediments since they enrich the bodies of water with nutrients, and in areas affected by periodic floods, they also enrich their agricultural fields. The process of silting is slow in human terms, therefore it is not identified as a real problem.

For these reasons the few successful reforestation projects in the high erodable areas of the Cofre de Perote are not done in an attempt to control erosion but as profitable competitive activities (for example, fruit tree plantations).

Neither deforestation nor erosion in the area is a problem for the shepherds. The clearing of the forest and the opening of new agricultural soils and their eventual abandonment are actions that produce new and better areas for grazing.

The private industrial entrepeneurs do not identify deforestation and erosion as a problem that could affect them, since there are no permanent forest industries in the area. Erosion is not identified as a serious problem for other industries in the region.

In contrast with these perceptions, deforestation of the Cofre de Perote has been identified as a problem by groups of urban citizens from nearby lower localities that blame deforestation as the cause for the water shortages in the cities and for the reduction of water in some springs of the area. They also impute deforestation to be the cause of "climatic changes" in the region. It is clear that these two problems are practically nonexistent, the first could be solved by having better water catchment structures and better distribution networks for urban villages, and the one referred to climate is a misunderstanding that has been spread throughout all Mexico and which lacks scientific basis.

In addition to this, it is known that deforestation increases the height of the water table in most of the cases that have been studied, with the possible exception of cloud forests, for its role in capturing precipitation and adding it to the water budget of the system (Hamilton & King, 1983).

Erosion caused by deforestation has also been identified as an environmental problem for the medium and long term by scientists working in the area (Golberg, 1983), especially since cloud forests of different types occur in the region.

These two groups of citizens (urbanites and scientists) provoke a different type of problem for the local and federal government officials, since they constitute an important citizen group of great influence over public opinion. This fact turns the deforestation problem into a political one. It is interesting to mention that deforestation, water shortages and erosion are popular subjects in the political discourse. If we add the fact that a large portion of the Cofre de Perote is a National Park, the situation becomes even more complicated.

These conflicting perceptions of the problem by different groups explain the failure of the very many reforestation (per-se) programs for the area, that are periodically proposed by state or national forest authorities, but that never have an echo from the inhabitants of the deforested sites.

As we can see from this case, the perception of different sectors of society on the role that forests play in the protection of the renewable natural resources, varies a lot within one region.

In this case one may also see the usefulness of analyzing the problem in order to find possible solutions.

It is clear that there is a great confusion and a lack of reliable information. Nevertheless, with the little existing data it is possible to identify concrete actions and the parties responsible for their execution.

As an example, I will mention some possible actions to be taken in this case.

SOME SOLUTIONS TO THE PROBLEM OF EROSION. The corrective actions should be: (1) the establishment of perennial crops on steep slopes, especially as buffer zones (tree belts) along water courses, and (2) the construction of terraces or other erosion control techniques. It will be necessary at the same time to stimulate conservation methods for sustained exploitation of the remaining forests or substitute them for tree plantations including agro-forestry systems. These corrective actions need investments, but those directly responsible (forest exploiters, farmers, cattle raisers) do not identify deforestation and erosion as their problem. They also lack the capital for carrying out the protective measures mentioned above. A completely different approach through economic incentives (low interest loans, subsidies, etc.) will be needed to accomplish the necessary actions. At the same time it will be necessary to have the appropriate legislation to regulate the use of land based on ecological, economic and agro-forestry studies in addition to the informed opinion of all people involved. But maybe the most important thing that will be needed is an efficient program of education, including an education extension program, for the region.

PROBLEM OF PROTECTION OF FLORA AND FAUNA. With the above suggested actions a large part of the biotic resources of the area may be better used and protected. In addition to this, it will be useful to revise the original Decree of the National Park of the Cofre de Perote and to make the necessary

changes to adapt it to the realities of the area.

Other actions from the State and Municipal Governments and also of private organizations to protect the biotic resources of the region should be stimulated.

As you can see, the solutions for each individual problem are not difficult to understand since they are so obvious. The implementation of the solutions is the limiting factor since all of them will affect economic interests and also will require considerable investments. The consequence of this is that nothing is done and deforestation and erosion continue. This attitude prevails for the region and for most of Mexico. And this is the reason for ever increasing deforested, erodable landscapes that occur in so many tropical regions.

FARMERS AND THE PROTECTION OF RESOURCES. Another important part of our analysis should be directed to the most important sector of the rural areas: the farmers living in them. Frequently development programs in the tropics are formulated in such a way that it seems as if the areas were uninhabited, when this is not the case. The tropical areas of low altitude in Mexico are inhabited by farmers, including the most remote ones. The tropical lowland areas, for example, of the Maya area have been inhabited continuously for over 3,000 years (Hammond, 1982).

It is clear that the perception of the farmer of forest exploitation, reforestation, use and management of their natural ecosystems, as well as their systems of agricultural production are often completely different from those of modern industrial society.

I will use the case of the Maya area to exemplify the importance of taking into account the traditional cultures to resolve some of the present problems in the management of the forest resources in the tropics.

MAYA SILVICULTURE. In the past few years several publications on the subsistence system of the old Maya have appeared (Darch, 1983; Flannery, 1982; Gómez-Pompa & Golley, 1981; Harrison & Turner, 1978; Turner & Harrison, 1983).

However the use of the tropical forests and the forest resources by the present and ancient Maya is a subject that has not been studied well, in spite of the enormous importance it has in the possible design of better systems for the management of the resources in the area (Barrera M. et al., 1977).

Unfortunately, ignoring the local inhabitants in developing programs for the tropics is a very widespread attitude.

The present day Maya and probably their ancestors use forest successions as a key technique in agriculture and silviculture. Plant and animal resources from successional fallows are very important in the subsistence economy of the present population of farmers, for they obtain firewood, wood, fruits, medicines, game, and materials for construction. With the management of secondary vegetation they obtain the recuperation of the fertility of their soils and control of their weeds and pests.

A very important fact to point out is that the knowledge of the value of biotic resources of the present Maya comes from their remote ancestors.

Unfortunately this appreciation tends to be forgotten due to the arrival of substitute products resulting from the modern industrial sector such as plastics, fertilizers, asphalt sheets, canned products, and registered medicines among others.

In spite of this cultural pressure in the Maya area there has been a strong

resistance that has allowed the survival of many uses and techniques coming from the ancient Maya. Some of them are about to disappear and perhaps many others have already done so.

On the other hand, it was once believed that the ancient Maya were important arboriculturists and silviculturists (Gómez-Pompa et al., 1984; Gómez-Pompa, 1987). It seems that the tropical forests had a greater importance for them. They depended on the forests for their subsistence and it seems that they were aware of their great potential.

Many of their basic products came from their forest ecosystems. The seeds of a forest tree of the Maya area, *Brosimum alicastrum*, provided them with an additional subsistence grain which probably was used as a complement to corn or a substitute for it in dry periods. The importance of this tree was mentioned by Puleston who suggested that this species was a fundamental resource that explains the success of the Maya culture in the past (Puleston, 1982). The same can be said for other wild fruit tree species of the tropical forest of the Maya such as: *Acrocomia mexicana, Annona squamosa, A. purpurea, A. muricata, A. reticulata, Byrsonima crassifolia, B. bucidaefolia, Calocarpum mammosum, Casimiroa edulis, Chrysophyllum cainito, Cordia dodecandra, Crescentia cujete, Diospyros digyna, Leucaena leucocephala, Lonchocarpus violaceus, Manilkara zapota, Parmentiera edulis, Persea americana, Pithecellobium dulce, Pouteria campechiana, Psidium guajava, Spondias mombin, S. purpurea, Talisia olivaeformis.*

Some authors in the past (Lundell, 1937; Puleston, 1968) suggested the possibility that the tropical forests of the Maya area with their abundance of useful species were certainly managed by the ancient Maya.

According to the studies on this subject, I believe that the forests we have at the present in most of the Maya area are the result of an ancient and complex tropical silviculture, developed by the ancient inhabitants of this region.

This hypothetical Maya silviculture (Gómez-Pompa, 1985b) consisted of a set of techniques integrated with their agricultural activities to cultivate, protect, and select tree species of economic, ecological, or cultural interest in all the region. It included the cultivation of a high number of trees in the backyards of their houses and ceremonial centers, in their forests and successions, and in special sites near their milpas, where they had forest gardens like the "petkot" (Gómez-Pompa et al., 1987).

The protection of useful trees in the slash and fall of the forests for their milpa cultivation was an important technique. The selection and protection of useful species (in the form of "stumps") that coppice during the slash was also an important technique. In addition the planting of trees in the milpas and their surroundings contributed to the presence of a useful forest flora. The protection and cultivation of trees and shrubs in the vegetation belt that protects the milpas (including the "guardaraya") also plays an important role in the tree management of the Maya. An important part of this silvicultural system is the management of their "natural" forests through selection and enrichment, by planting useful species. The Maya of today as well as their ancestors observed and experimented with their wild biota discovering uses for most of the plant species. Those of greater value were probably semi-domesticated in their dooryard gardens.

These combined techniques provided them with abundant forest products for their subsistence and at the

same time biological diversity was preserved. The activities of biological conservation of the Maya were mainly a matter of practical survival, mixed with superstitions and other beliefs.

The possibility that the old Maya gave value to the conservation of biological diversity can not be disregarded, mainly if we take into consideration the precise knowledge they had of their wild biota shown in the rich biological nomenclature of their folk taxonomy (Barrera M. et al., 1976) and in the vast knowledge of the possible uses of practically all their flora (Mendieta & Amo, 1981; Roys, 1931).

The present Maya, inheritors of this technology, have given us the clues to reconstruct the silviculture since they still have many of the ancient practices, although not integrated in any one place.

The dooryard gardens where several "wild" species including the famous "ramón" (*Brosimum alicastrum*) mentioned before are cultivated and protected, are a good example (Smith & Cameron, 1977).

The tropical forests of the Maya area, that are being deforested in colonization projects and in forest exploitations that have been going on for decades, are the product of an advanced ancient silviculture of the old Maya.

Unfortunately the present day Maya farmers, inheritors of that silviculture, which in part they still preserve, cannot use those techniques and methodology since the modern industrial society requires the trees of their ancient "selvas huerto" (forest gardens) for their industries, and the soils for grazing lands. And probably in the future they will dedicate them to monspecific forest plantations. What incongruency!

Obviously, we have before us two different cultures, the traditional (past and present) and the modern industrial one, each with different values and perceptions of the importance, use, and conservation of the forest resources. It is clear that if we want to make a change in the present tendencies we will have to consider the two worlds and try to make compatible the conflicts of interest and of values.

It is evident too, who has the responsibility of being aware and taking the first steps.

SOME FINAL CONSIDERATIONS. Due to all I have mentioned before, it becomes quite clear that a profound change is needed in our approach to the problem of deforestation in countries where these two cultural worlds co-exist.

The present approach of ignoring traditional methods of management of resources seems to me erroneous, as erroneous as it is to try to impose new and often inefficient methods. These mistakes have led us to a considerable loss of tropical forest resources that endanger the biological heritage of the tropics.

I suggest that the plans and programs for forest development in countries where fortunately the two cultures coexist, should foresee different actions and approaches for the two realities. The approach and objectives of forest research, education, extension and development should be adapted to the two cultural worlds. The human and economic resources should be equally invested in the development and technological improvement of both approaches.

The first approach should correspond to what I call Maya Silviculture, and be oriented toward the improvement and gradual intensification of the traditional silvicultural practices with techniques either traditional or modern,

including low investment and intensive hand labor. Examples of activities that are suggested for the support of this approach would be:

1. The study and selection of protected species in the felling process. This selection would be made in direct contact with the local communities and according to their needs.
2. The study and selection of useful tree and shrub species of rapid growth that can be selected and protected. The selection can be made in relation to their direct use such as food, construction, medicine, etc; or through their role in the fallow; or for their advantages as green manure or for the quality of the nutrients in ashes for the next milpa.
3. The selection of forest species and a mixture of them that could be planted during the agriculture seeding to establish an artificial forest (for example the Taungya-system).
4. Protection and development of small forest areas like the Maya "pet-kot" and the Huastec "te lom" (Alcorn, 1984) near the milpa.
5. Study on optimization of architectural designs and production in dooryard gardens, also on mechanisms for industrializing and commercializing their products.
6. Selections and improvements of tree species in the dooryard gardens (Fig. 3) according to local needs and possible markets.
7. Development of small forest units (managed tropical forests) based on the management of natural tropical forests.
8. Study of the local agroforestry systems to evaluate their economic and ecological efficiency and to suggest improvements to them (for example, study of the wild Leguminosae used as shade in coffee and cacao plantations, etc.).
9. The evaluation of modern technical advances and their possible adaptation to Maya Silviculture.

This point of view on silviculture should include as an indispensable part, the formation of professionals, technicians, extensionists, researchers and promoters who would have as a main focus of their education this approach in addition to modern silviculture and ecology.

The other approach would be the one for the industrial silviculture which would be directed mainly toward forest plantations to supply the demand of industries. Its main land competitor will be commercial agriculture and cattle raising activities.

The main problems that last approach will have to face would be:

1. The problem of long term investments in poor countries.
2. The low profitability of short and medium term of forest plantations in comparison with other agricultural and cattle raising activities.
3. The need for large areas generating conflicts with the urgent need of land for landless farmers.
4. The problem of pests and weeds, inherent to all monocultures, especially in the tropics.

This dual system of forest research and development that I propose may be an alternative solution to the deforestation problem of the tropics and also an alternative tool for a more realistic and ecologically sound development for many underdeveloped regions of the world. An example of the possibilities of this approach can be found in the interesting work that recently has been done in tropical agriculture at the IITA

(International Institute of Tropical Agriculture in Nigeria) in the study and development of new farming systems based on traditional techniques (Wilson & Kang, 1981) and also those of the IRRI (International Rice Research Institute in the Philippines) on traditional farming systems. I must not forget to mention the contributions from my own institution, INIREB (National Research Institute of Biotic Resources in Mexico), on the study of the traditional "chinampa" agriculture and its transference to the tropics (Gómez-Pompa et al., 1982).

To end, I must repeat that the natural forest ecosystems in the tropics are in great danger. The problem has been mentioned and analyzed over and over again in many forums. It is time to follow a more aggressive and realistic approach in tropical forestry and in this approach the ancient Maya Silviculture may help us to see the future.

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Changing Maya Livelihood in the Forest of Quintana Roo: Flexibility and Freedom

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The forest of the Yucatan Peninsula has represented many different things to people over the centuries since the Spanish conquest—to the people who have lived in it, contemplated it from the shifting boundary of its frontier, or shaped plans and policy with regard to it. At times and for some it promised refuge from the exactions of Spanish overlords and clerics, and from their nineteenth- and twentieth-century counterparts. For still others it was a sinister hideaway of indolent, heathen and rebel Indians. While some fled from the settled towns and villages of Yucatan to begin new lives in the vast expanses of sparsely-populated and unadministered forest—driven there by war, epidemic, famine, drought and the multiple burdens of colonial town life and post-colonial plantation laboring—others were sent there at gun point to end their days in misery as soldiers and political prisoners—fighting hostile Indians, noxious snakes and insects, disease and malnutrition all the while laboring for the profit of corrupt civil and military officials. For the Maya peasants who have made it their home, the forest has long been the matrix of their livelihood as slash-and-burn farmers and forest hunter-gatherers. For still others, some of them Maya too, the forest has been a resource of commercial value, the source of semi-tropical forest commodities which have found increasing demand in national and international markets. Livelihood and sudden prosperity, the means for living and a way of killing, a haven and an exile, a sacred place and a place of chicle-gathering camps and terminal points of international trade networks, the frontier of Spanish- and English-ruled worlds and the heartland of autonomous Indian rebels and fugitives—the forest of the Yucatan Peninsula has been all of these and more during the last five centuries on into the present. And the forest has been changed for all of it, too.

Those who have studied the people of the Yucatan Peninsula, whatever the topic or historical period of their researches, have inevitably had to consider the forest. Political and economic history, missionization and religious change, agriculture, temple building and the decline of a civilization, the history of wars and revolutions, as well as concerns about development and the future—these are each stories about human endeavors and human potentials both enabled and constrained by the existence of the forest. They are stories too about human actions which have and will change the forest, for better or for worse. It is far beyond the purposes of this paper to review the many links established between historical processes of social and cultural change and the environment of Yucatan. For now the point is simply this: that any human action which relies upon the forest, and which subsequently alters it, has multiple ramifications in other and subsequent realms of life and livelihood. Changing uses of the forest by those who live within it and those who come to exploit it, though agro-economic in their most narrow sense, sooner or later evoke for all con-

cerned grander issues of freedom and slavery, peace and war, progress and decline. Such was the case, at least, in my own studies of agricultural change among forest-dwelling slash-and-burn corn farmers of central Quintana Roo; perhaps then this case will serve to instantiate the more general point of this paper, a point to which I will return later.

Agricultural Change: Intensification and Diversification

Observations made during fieldwork in the late 1970's among Maya Indians of central Quintana Roo indicated that corn farmers of that region were diversifying their repertoire of agricultural practices, in particular through adoption of small-scale irrigated gardening. While minor developments in and of themselves, those observations coincided with fragmentary reports of numerous field investigators over the last half century, suggesting a general trend under way towards the intensification of agriculture in the forested lowlands of the Yucatan Peninsula (Sullivan 1983).[1]

Though slash-and-burn cultivation of maize has long been the principal productive activity of Mayas in the broad expanse of the forested lowlands (outside, that is, the henequen-producing areas of the state of Yucatan itself), over the last decade or so archeologists have amassed considerable evidence for the ancient practice of various forms of intensive cultivation— raised fields, terracing, fencing, swamp drainage, among others. Hence, a trend towards intensive cultivation in the present should perhaps be spoken of as re-intensification. By the term "intensification" I refer to related changes in land use, laboring, and techniques of cultivation—a shortening or elimination of rotational fallowing, an increase in units of labor expended per unit of area cultivated, an increase in the use of capital and the creation of permanent or semipermanent agricultural infra-structure (cf. Boserup, 1965; Brookfield, 1972; Turner and Doolittle, 1978). It is of little analytical value to simply dub a particular form of cultivation or a system of agricultural tasks as "intensive"; what is or is not an intensive practice is relative, after all, to other practices actual or potential, past and present. "Intensification" however, encompasses not only actual practice but the historical development of contemporary practices. Within an historical perspective upon agricultural practices and land and forest usages, it is a label for a set of related trends and developments; the use of the term signals that our analysis will consider the relationships between contemporary practices, the multiple factors which have shaped them, and the varied consequences of them.

The potential impact of intensification or re-intensification upon both Maya household economies and upon local forest ecology would be complex and no doubt significant. From that expectation derived a project to document the multiple forms of such intensive cultivation, the distribution of their practice among communities and among cultivating households in individual communities, their relative importance and the factors promoting their development among people otherwise dedicated to extensive subsistence-

[1]I realize that the term "intensification" as applied to agricultural change in Yucatan has been used elsewhere to refer to another aspect of that change: the shortening of fallow periods in corn farming itself, along with reduction in the number of species and varieties of plants cultivated through intercropping with corn (cf. Alonso 1979).

oriented swidden farming. The region of interest in this regard included central Quintana Roo, particularly those parts bordering upon southern and western Yucatan—an area undergoing repopulation since its abandonment during a nineteenth-century Indian war.

That research is ongoing and these results are, therefore, preliminary. In the meantime a major study of related developments in southern Yucatan's Puuc Hills region has appeared (Ewell, 1984) as well. The results of fieldwork in central Quintana Roo have revealed, however, a significant though instructive flaw in the original conception of the research. Simply stated, it underestimated the flexibility of those slash-and-burn farmers to annually allocate their productive labors (as well as other personal and collectively-disposed resources) among various production and income-generating alternatives, and to do so in ways which do not foreclose future options (those of the next season or future years). Though quite independent of the process by which I came to think and write about flexibility of Maya agriculturalists, it is surely no coincidence that Ewell has arrived at and written about farmers in the Puuc Hills region in strikingly similar terms—there are differences of note, as well.

The flexibility of slash-and-burn corn farmers in central Quintana Roo is evident enough with regard to annual changes in acreage under cultivation, for example; or with regard to the location and number of cultivated plots. Mayas of central Quintana Roo are shifting cultivators insofar as they annually work in different forest locations. They do not move settlements, however, so the term "shifting" is used here in a manner like that of Carter (1969:130). And factors beyond the exclusive control of the cultivators introduce still further degrees of variability in each season's round of agricultural activities. Annual variations in the timing of rains affects the scheduling of labor in agricultural tasks, while the quality of the burn in slash-and-burn systems also affects the timing, difficulty, and outcome of most subsequent tasks as well. These are well-known sources of variability in the practice of swidden cultivation on the Yucatan Peninsula—features which methods in the study of such a system must be adapted to take into account. See, for example, Thompson (1974:59) on the effect of inadequate rainfall on at least temporary migratory wage employment; Redfield and Villa (1962:52) and Steggerda (1941:113, 134) on annual variation in yields and acreage under swidden cultivation; and Conklin (1963) on general considerations of variation in the parameters of swidden systems. The data of a single season, though it be collected from many cultivating households, may seriously misrepresent either multi-season averages or trends in acreage under cultivation, yields, and so on. And during a single season, small differences in the timing of each household's activities can produce marked differences in the success of that season's efforts—though a season be a good one in terms of the arrival of rains and the absence of serious plant diseases and pest infestations, a household that is a few days late in burning their field in anticipation of planting can find itself having a disastrous agricultural year.

The phrase "intensive agriculture" or "intensive cultivation" suggests, often, the at least partial abandonment of such variability and flexibility. Speaking for the moment of irrigated works in particular, without regard to their size or scale: there is now infrastructure

to maintain, there are allocated rights to water and land that must be managed and defended, there is a reduction or elimination of fallow periods; and there are new expenses incurred in obtaining seed, chemical imputs, machinery, tubing, and so forth—debts incurred which can give others interest in and some control over production processes. There is, in a word, constraint to the drastic reduction or expansion, not to mention relocation, of the sites under irrigation. That, at least, is to be expected. Ewell has described the varying degrees of these and other constraints upon different types of irrigation units in Yucatan (1984).

When cultivators in central Quintana Roo begin to allocate at least a part of their labor to intensive cultivation on a small scale, however, they do not necessarily surrender the annual flexibility which characterized their once more exclusively swidden regime. Irrigated houselot gardens, larger irrigated truck gardens, and even multihousehold irrigation units constitute part of what it is to make a living in many contemporary Maya communities of central Quintana Roo. But these are forms of cultivation whose features—acreage, cultigens, scheduling, chemical imputs, and product disposition, etc.—are themselves quite variable within certain limits. Cultivators in central Quintana Roo may shift from work in intensive cultivation to work in more extensive cultivation either during the course of one season, or from one agricultural season to the next. Their ability and their need to do so derive from the nature of the intensive and extensive systems of cultivation which they practice. They derive as well from the cultivators' individual and collective experiences with diverse forms and conditions of laboring over long periods of time. Erratic yields from rain-fed agriculture, the instability of price which has plagued some agricultural commodities, changing funding levels of government programs in agricultural and forestry development, the attraction of temporary, alternative wage-earning opportunities in distant towns and tourist centers—these are all factors of the first sort in the nature of the intensive and extensive agricultural systems within the context of contemporary Quintana Roo economy. A vivid oral history of forced labor on the agricultural and cattle estates of Yucatan, the vestigial hostility toward non-Mayas born of that experience and the experience of a long and bloody war, and an understanding these people have concerning the transitory nature of things as they are at present—these are factors of the second sort, part of individual and collective experiences in the world.

The flexibility mentioned earlier is a product of the interaction of such factors, and it can be studied in terms of them. Presented below, then, is the evidence and the nature of that flexibility, and a discussion of the problem it raises for considering agricultural trends in the region in terms of such concepts as intensification and its obverse, disintensification. Finally, and in keeping with the broader issues of forest use and the nature of the forest for those who work and live in it—issues hinted at earlier in this paper—some ideas will be offered concerning the relationship of this observed flexibility and the preservation of the forest matrix of Maya livelihood and freedom. First, though, some information must be provided about the people and places of this study.

Maya Communities and Cultivators of Central Quintana Roo

The area under study lies roughly within the two adjoining municipalities of Felipe Carrillo Puerto and José María Morelos, Quintana Roo. In this area of approximately seven thousand square miles there are fifty-one thousand people (about seven people per square mile) living in some two hundred and fifty settlements. Most of the settlements are situated on *ejido* land, land granted through application of the Federal Agrarian Reform; there is very little private property in land and forest in this part of the Yucatan Peninsula. Though agrarian censuses count some two to three hundred lots on which cattle are raised with pasture accounting for lesss than two percent of the area under consideration here (Quintana Roo, 1982:92), slash-and-burn maize cultivation is the principal productive activity within this region still largely covered by a low, semideciduous forest. Most of this forest, it seems, has been felled at least once within the last twenty years.

Most people who live in these settlements are descendants of fugitives and rebels who fled to the virtually uninhabited forest during the nineteenth-century Indian rebellion known as the War of the Castes (Reed, 1964). Perhaps as many as one hundred thousand Mayas entered the southern and eastern forest during that war, though by 1915 their number had declined to probably no more than five thousand in all of what is today the State of Quintana Roo (making for about five people per hundred square miles).

The work of Mexican anthropologist Alfonso Villa Rojas, who conducted fieldwork in central Quintana Roo during the mid-1930's, provided the first detailed study of those forest-dwelling Maya. What Villa had to say about Maya agriculture as it was in the 1935 and 1936 seasons is of particular interest here. At that time the average area farmed per household—via slash-and-burn methods—was about nine acres (or five acres per laborer). Villa reported yields of corn averaging between four and nine tenths of a metric ton per acre in what he called virgin soil; roughly half that was obtained in plots farmed for a second consecutive year or on a short fallow rotation (i.e. less than ten years between cultivations). He further noted that almost eighty percent of the farmers planted at least some of their corn in long fallowed or "virgin" forest lands, accounting thus for forty percent of the total area under cultivation (Villa Rojas, 1945:61). Mayas who Villa studied were, in other words, farming in what was at that time long-fallowed, virtually abandoned forest.

They were enjoying good yields of corn for their efforts; close to five metric tons of corn were harvested per household per season. Villa was careful to note that the figures he provided reflected the harvests of relatively good years, those in which rains had come in sufficient quantity and with due spacing. Yet the harvest of such good years was sufficient to tide a household over the inevitable two or three lean years as well, since in those days little corn was taken to market. Villa found the average man spending only one hundred and forty days of the year in agricultural labor during the 1935-1936 season; and only one hundred and eighty-six days per year were spent in all productive activities, agricultural as well as non-ag-

ricultural—the latter included bee keeping, chicle gathering, and hunting, in particular (Villa Rojas, 1945:77).

Today, few if any Mayas make a living through slash-and-burn corn farming alone. Hunting, chicle gathering, commercial apiculture, houselot and truck gardening, and often laboring for wages in town or on government-sponsored rural development projects are essential elements of the economic activities of any viable Maya household. And for still others, cattle raising, wholesale and retail marketing, and lumbering are important. Largely absent are the craft industries widely reported for Maya communities in parts of Yucatan. That absence notwithstanding, Maya household economy and Maya work histories are as complex in central Quintana Roo as those reported for other parts of the peninsula (Alonso, 1979; Ewell, 1984:142).

Slash-and-burn farming has changed subtly over the years, and the change has been significant. It is partially responsible for people's present-day search for alternative means to livelihood; it is partly a result of that search. When asked today what the corn yield in a "good" season would be, people of the region most often cite the native equivalents of four-tenths of a metric ton per acre. That is precisely the yield which Villa reported as the average for the mid-1930's. But that yield, in fact, is seldom obtained anymore. During the first year of my field research in central Quintana Roo, corn yields were pitifully low—little higher than one-hundreth metric ton per acre. That was in 1978. As the harvest of 1979 came in, people spoke of it as a relatively good year, though yields were still as low as a tenth of a metric ton per acre for some households. The areas under cultivation were substantially greater than they had been back in 1935, however—up fourteen percent per household and seventy percent per laborer. In the early 1980's harvests were reportedly even better, approaching what is locally considered optimal. But one or more seasons of poor yields had led, in turn, to reduced acreage under cultivation. Would-be cultivators had to temporarily seek income elsewhere, working for wages in town, in road construction, at Caribbean resorts, and elsewhere. And some had become wary of spending cash to expand area under cultivation through the hiring of laborers among their neighbors, relatives and acquaintances. So even what were called "good" years were poor agricultural years for many farming households.

Though for reasons mentioned earlier the data of even several seasons of slash-and-burn cultivation may misrepresent significant trends in yields and areas under cultivation, my field data at least coincided with numerous reports made by cultivators themselves to the effect that these years they are working longer in agricultural labors but getting less for it than they or their predecessors did as recently as several decades ago. The factors behind such an apparent long-term decline in the viability of slash-and-burn agriculture in central Quintana Roo are no doubt numerous (Sullivan, 1983). What is more relevant here, however, is that Maya mention the fact of that decline when they speak of their search for new forms and techniques of agricultural production—particularly when they express interest in forms involving irrigation on a small scale of marketable crops of vegetables and fruits.

Contemporary Alternatives in Intensive Cultivation

Small-scale irrigated cultivation in central Quintana Roo at present takes three related forms—houselot gardens in raised beds with associated cribs or platforms (called *ca'anche'*), gardens which cover at most a few hundreds of square feet; larger truck gardens ranging up to almost half an acre in area; and collective or multihousehold irrigation units ranging in size from two and a half to twenty acres or more, often but not always established and maintained under supervision of one or more government agencies concerned either with agriculture or Indians. The picture of agriculture and agricultural change in central Quintana Roo involves more than just those three forms and scales of irrigated gardening. But those three forms are closely interrelated in ways which go beyond the fact that they each involve dry-season applications of water to crops other than the staples maize and beans. The nature of their interrelations will be made clear shortly. First, some further description of each form and scale of irrigated cultivation is in order.

All of the land and the forest of central Quintana Roo has been subject to the Federal Agrarian Reform and made accessible to cultivators only by virtue of their membership in one or another agrarian community. (There are a few private ranches in the area, seasonally occupied by corn farmers and small-scale cattle raisers, people who are otherwise also members of agrarian communities.) Except for the largest of towns in the region, while communities have access under federal law to areas of the forest varying in extent in accordance with their respective populations (grants range from ten to three hundred square miles), they include settlement areas of rather uniform size—about one hundred and twenty-five acres for houses, houselots, stores, roads, schools, churches and parks. Much of the settlement area is in turn divided into houselots of uniform size approaching the maximum allowed under the agrarian reform, six-tenths of an acre. Very little of the houselot space is occupied by the house structures and the shelters and corrals of domestic livestock.

Whether any of the remaining portion of the houselot is cultivated depends upon several factors, the most important being the quality of the land itself. Some lots are simply too rocky; though ideal for dry houses, they are unsuitable for gardens and orchards of any but the smallest size. Most houselots, however, are at least partially cultivable without extensive modification of their topography by terracing, for example. They all contain at least a few trees for fruit or shade, as is typical of houselots throughout the Maya lowlands (See, for example, Smith and Cameron, 1977; Wilken, 1971:441; Ewell, 1984). On the other hand, one seldom finds staple crops such as corn and beans cultivated within the boundaries of a houselot, except for those on the edge of villages, opening into adjacent cultivated forest clearings.

A variety of vegetables for home consumption and market are cultivated within the walls of houselots. Radishes, onions, cabbage, lettuce, garlic, and coriander may be cultivated in rectangular earthen beds approximately six to ten feet long and some ten inches to a foot deep. Maya speakers refer to these beds by the Spanish word *era*, and they were taught this form of gardening about ten years ago by extension agents of the Department of Public Education. Mayas in

the State of Yucatan have apparently been making them for decades, on the other hand (Redfield and Villa, 1962:46). Preparation of the beds involves loosening the thin soil of houselots, removing stones, and gathering from elsewhere black soil which will be mixed with the houselot soil in order to form a more fertile garden matrix. The beds are constructed anew each dry season through the labor of both men and women in a household; their watering and tending thereafter, however, is primarily the dry-season activity of women. Women also are the ones who periodically harvest the beds and take small quantities of the produce to market for sale. These gardens are almost nowhere to be found during the months of the rainy season.

Tomatoes, varieties of chile, and watermelons are also cultivated in houselots, though not in the beds just described. Rather, they are planted in rows of serial, shallow depressions called *pozetas* "little wells." These are not exclusively dry season crops—particularly not the chile which yields for more than a single year. The cultivation of such crops in irrigated *pozetas* is a development even more recent than the cultivation of raised beds; it results from recent experiences of Mayas in government-sponsored multihousehold irrigation units. More about that shortly. (It should also be mentioned that these crops have long had their intercropped, rain-fed counterparts as part of traditional slash-and-burn corn farming in Yucatan and Quintana Roo.)

One further feature of houselot cultivation must here be mentioned—cultivation of herbs, seedlings, and small vegetables in raised cribs or platforms called *ca'anche'*. Such cribs stand chest-high and may be as small as twenty-five or as large as fifty-five square feet, rarely larger still. The cribs are filled with five to six inches of a rather average variety of local soil called *kancab* (slightly reddish-orange in color) topped with another five to six inches of a more scarce and valued black soil brought to the houselot from the hollows of forest hillocks or from the base of trees where horses and mules are usually tethered. A variety of herbs, both culinary and medicinal, are planted in these cribs, along with small quantities of produce for market and for household consumption. They include garlic, onions, and tomatoes as the most important marketable produce. Finally, some crops destined for transplanted intercropping in cornfields—for example a variety of chile which is grown in the cornfield under rain-fed conditions—may be first planted as seed in the cribs or even in the beds described earlier. Raised platform cultivation of this sort is decidedly *not* a recent development, nor is it local, though its uses in other parts of Yucatan vary widely (Wauchope, 1938:132-33; Redfield and Villa, 1962:46; Vargas, 1983).

Raised beds, rows of *pozetas* and one, two or even three crib platforms are watered during the dry season either by hand-drawn well water or by water supplied through potable water systems at houselot outlets. The cultivation of such gardens is primarily a dry season activity and the work of women.

Truck gardens and sites of permanent cultivation. At the peripheries of villages may be found unoccupied houselots under dry season irrigated cultivation. Though still lots cultivated by individual households, the scale of cultivation now exceeds that possible within most occupied houselots. Of such peripheral lots given over to truck gardening, I have found some ranging in size from five thousand square feet to over half

an acre. The crops planted in them are irrigated by hand-drawn well water or by water carried in buckets from the nearest outlet of a village's potable water system. Currently, watermelons are the crop most commonly chosen for cultivation in such irrigated lots. The crop is destined for sale, either in village or town. But there can be just as great a variety of plants cultivated in such peripheral lots as there are in houselots on the one hand and cornfields, for example, on the other. In one such lot I found under simultaneous cultivation not only watermelons, but also cantelope, pineapple, sugarcane, onions, radishes, squash, manioc, yucca, tomatoes, a very small number of corn plants, and several young fruit trees including bananas, mammey, custard apple, and limes. There were also several other edible leaf plants and herbs. Such single-family irrigated lots are not yet very common in the region of this study; it is unusual to find more than several in a village of even a hundred households.

Irrigated lots of comparable size cultivated by individual households may also be found well beyond the village perimeter (and therefore beyond access to the potable water network). These are located in or near what locally are called ranches (*ranchos*, even in Maya), though by this term is not meant fenced tracts of private property devoted to cattle raising. Rather, such ranches are something more akin to seasonally-occupied hamlets utilized by several related households who make their cornfields and tend their bee hives (perhaps even usually hunt) in that particular part of the forest year in and year out. In the past some Mayas kept one or two hundred head of cattle on fenced pastures in the immediate vicinity of such ranch hamlets; but while such cattle raising is for the most part a thing of the past, the ranches continue to serve as domiciles far from the main settlement but close to customary work sites—very handy during harvest time for example. And those sites include small areas of irrigated gardening, as well. Ranches are always situated near abandoned wells or water-filled sink holes (*cenotes*), so their occupants have the option of preparing beds or rows of *pozetas*, cribs, and other kinds of small gardens much like those found in the main settlement's houselots. Those gardens may in fact be somewhat larger than is customary for houselots—longer beds, more chile plants, and so forth—yet still smaller than those of the multihousehold irrigation units from which the techniques of their cultivation in part derived.

Multihousehold irrigation units. Between 1977 and 1982 both federal and local government were actively encouraging and supporting the start-up of multihousehold irrigation units throughout central Quintana Roo. In the community which I came to know best, a village called Tuzik, men from fifteen households worked under the direction of several local and federal agencies to begin just such a project. The unit was five miles east of the main settlement, on the only tract of more fertile black earth to be found anywhere within that part of the forest. The site was chosen also for its deep well, the abandoned water source of a colonial-era or perhaps nineteenth-century ranch. To facilitate the project the government financed construction of an all-weather road running from the main settlement to the irrigation site; and over the years which followed, they provided seeds, cuttings, fertilizer, and other chemical inputs, a water pump and plastic tubing, hand tools, and small

amounts of food and credit. Agronomists visited the site regularly and employees of the National Indian Institute provided some marketing advice and, for a while at least, free transportation to the marketplaces of distant tourist centers of the state.

For those Maya cultivators who joined the project, the work of the irrigation unit marked a radical change in production organization and techniques. Men of the unit (after the first year their number had dropped to ten) worked collectively at a wide variety of new tasks—digging the *pozetas* in which to plant new varieties of tomatoes and chile, for example; applying fertilizer, insecticides, and herbicides—materials which they had never handled before; hauling water and redirecting tubing and hoses; constructing seed beds and transplanting seedlings, and so on. And they had to learn how to operate and perform minor maintenance on the mechanical pump. It was only the final income from the sale of the unit's produce which was distributed among the members, along with unsalable produce, that is. The men chose irrigation unit officers so that their names might duly appear at the bottom of the many petitions they prepared for government assistance; but in practice decisions were made collectively at frequent, informal meetings of all unit members. There was no differentiation among the men with regard to the nature of the tasks they performed nor the share of the proceeds which they took. No women worked at the unit.

During much of the first two years of the unit's development, men worked at it five or six days each week, returning late every afternoon to their homes in the main settlement. Some had other business in that part of the forest as well—their cornfields and bee hives, for example.

The men of the unit originally planned to clear and cultivate up to two hundred and fifty irrigated acres. At the end of their first year's labors, however, they had planted only twenty acres, those in watermelon, chile, melons, and fruit trees; in the subsequent year tomatoes were added to this short list. The area cleared and under cultivation at this unit never came to exceed those initial twenty acres.

Other options. There are many other alternative production and/or income generating activities to which Maya cultivators of this region have recourse. They may expand on their bee keeping, raise a few head of cattle and pigs, participate in the seasonal gathering of the latex of the sapodilla tree (chicle), function as middlemen in the regional trade in forest produce, or dedicate themselves more regularly to the nocturnal hunt for deer and other game. They may also hire themselves out as wage laborers in agriculture to people much like themselves either there in their own communities, or in others; or they may seek wage labor still elsewhere, particularly in road and building construction. They may emigrate seasonally to sugarcane producing regions in the south of the state, or permanently relocate to one of the growing tourist centers in the north. These are just some of the ways people of the region either supplement their primary production efforts in slash-and-burn corn farming or opt out of that way of life altogether. My cursory listing of these as "options" is not meant to imply that individuals can choose freely and casually among them, as though each did not have its own particular constraints and limitations. I simply mention them as part of the total picture of agricultural change in central Quintana Roo.

Strategic Flexibility

A preliminary survey of forms of intensive cultivation in central Quintana Roo has revealed a more complex picture of agricultural change than was anticipated on the basis of earlier research.[2] As expected there were many communities where multihousehold irrigation units could be found. But there was little evidence justifying talk of a *trend* either towards or away from reliance on that particular form of intensive cultivation. In some communities small irrigation units, working with either pump- or hand-drawn water, had been functioning for only a year or so, but seemed to be doing well. During the summer of 1984 there were units of as few as three men (Dzoyola) and as large as twelve (Yaxley) harvesting tomatoes and watermelons, more often than not from fields irrigated by hand-drawn water. In other communities, however, such labors had been abandoned already. Twenty-five men left the ten acres they had cleared when their pump broke down in the midst of the dry season, and the crop was lost (San Felipe Barriozabal); in another community (Saban) twenty acres were abandoned for similar reasons. And finally, in some communities similar problems had led to the suspension but not, it seemed, complete abandonment of irrigated cultivations—weeding of fruit trees continued, regrowth was cut back from time to time, while project members continued to solicit government aid to restart the full operation of their units (Xcantzepchen, Tuzik).

Tuzik was one of those places in which the irrigation unit begun some years earlier was by 1984 in a state of abandonment. The fifteen men who had started the unit back in 1978 had been prompted to do so both by the dearth of corn in those years of very poor harvests, and by the promise of higher incomes through this new agricultural activity. But the group in fact never realized those higher incomes, nor did they find the burden of their labors lessened. On the contrary, those men working with the irrigation unit found that their efforts need by constant and unrelenting, and that the labor was tedious at that—hauling water from a deep well several hours every morning and afternoon, day after day, for months on end (the pump had yet to be installed); weeding and fumigating and guarding irrigated tracts against various kinds of pests; clearing new tracts for the expansion of the unit; preparing seed beds and re-planting once those beds had had their seedlings removed and transplanted. And the work required a new labor discipline—plants would die if not watered regularly (watering now a man-made rather than natural event); insect and animal pests would thrive if not held in check; and the interest and support of government might wane if the pace of the unit's work were seen to appreciably lag. The work schedule and discipline required for irrigation was markedly different in kind from those to which these once autonomous slash-and-burn corn farmers have long been accustomed. That fact was given formal and succinct expression by the members of the irrigation unit themselves when they found it necessary to establish and sign the following written agreement:

[2]Communities visited for the purposes of the survey of intensive cultivation included San Felipe Barriozabal, Dzoyolá, Yaxley, Sabán, Xtrapich, Dzulá, San Francisco Aké, Filomena Mata, Tuzik, Chan Chen Comandante, Melchor Ocampo, Xa'an, and Xcantzepchen.

Act of Agreement

The 24th of April of 1979 there took place a meeting of the members of the irrigation unit of the ex-hacienda of San Antonio. Those who sign below express their conformity with the agreements of that meeting concerning how to continue the work at the irrigation unit. Said agreements are: 1) That on Mondays begins the work and the work continues daily until Friday; 2) That if a day of work is lost between Monday and Friday, that day is made up on Sunday.

Long past, it seems, were the times when half a year's effort alone—efforts scheduled according to nature and one's own inclinations alone—might provide for the substantial portion of the household's subsistence needs. Despite their hard labors— eased a bit when a pump was finally provided and a large water storage tank was constructed—the work was far less rewarding than the unit's members had expected. The prices of their produce were unstable. At the same time that they encouraged men of Tuzik to turn to irrigated agriculture, those concerned with the economic development of the region were promoting similar activities in at least seven other nearby communities. When watermelons were ready for market from Tuzik, they were arriving in town from half a dozen other units as well; as a result the price fell with short-term gluts. So too with chile and tomatoes in their turn. Late in the second year of the project, members of the irrigation unit were going further and further afield to sell their produce. Yet still they found market gluts and few buyers. They considered converting much of the area then under irrigation to a less labor-demanding orchard regime.

That, eventually, is just what they did in Tuzik, at least until their pump ceased functioning. In the meantime the number of households involved in the project declined to three, and those left found themselves unable to keep up with the weeding required (given that they still had their other productive activities to attend to as well); by the summer of 1984 they were considering asking the government to assist them with credit to either hire the necessary labor, or to remunerate themselves while they do the weeding.

But, as I suggested earlier, one cannot discuss agricultural change in Quintana Roo while only focusing upon one household, one project, or even one community. Many irrigation projects went into decline, and for very similar reasons. But at the same time new ones were starting up, some spontaneously, rather than under government sponsorship. In the 1980's the federal government brought to Quintana Roo a new agricultural and forestry development program which dwarfed in scale those of the late 1970's irrigation schemes, and which took root in many communities alongside the either nascent or moribund irrigation units. COPLAMAR was the name of a project which combined in multihousehold production units the production of corn, small amounts of irrigated tomatoes and chile, cattle raising, reforestation (in marketable species such as cedar) and some orchard culture. Men were paid weekly wages for their labor in the unit, as long as there was money in the program's budget, that is. The money ran out in the middle of 1984, however, in the midst of the nation-wide financial crisis of that year. Work ground to a halt; some COPLAMAR assets were seized by peasants in various communities, peasants claiming several

weeks overdue wages. The project appeared destined for dissolution.

It is beyond the purposes of this short paper to assess the successes and failures of government-sponsored projects in Quintana Roo. The point here, rather, is simply this: the projects and the employment which they generate, from the point of view of cultivators in the region, come and go like the seasons themselves. Or perhaps over longer periods of time one can liken the comings and goings of the projects to climatic changes of a transitory but multiseason sort. Both affect the allocation of labor among various possible productive tasks and pursuits in the forests and the towns. Both produce, in that sense, patterns of shifting agricultural activity and shifting labor use in general. And both have their local variations as well—just as the rain can fall and slash-and-burn cultivation succeed in one community, while cultivators fail miserably in the next, so too a project can be in decline in one locality and in ascendancy in the next. Perhaps, one might say, this is all just part of unstable government finances in the 1980's, or the inevitable result of trial and error in agricultural development—something which in the long run will yet produce permanent changes in productive infrastructure and agricultural practice. But as the years pass and the short run becomes the long, an entire generation of cultivators is raised in a world where among the unpredictable factors governing the nature and success of their laboring are added the effects of markets, federal budgets, international debt, taxation, and the changing state of the art in tropical forest development. Such people remain shifting cultivators of a kind, though they leave behind a once exclusive reliance upon slash-and-burn techniques.

There is a second point about this apparent flexibility in the annual disposition of labor by Maya cultivators of central Quintana Roo: flexible is just how they want things, for the time being at least. They are not people who have occupations such as we do. People in the region do not labor at their *job* and experience periods of employment and unemployment, for example, as the market for their labor evolves. These are people for whom laboring is a way of life, a way of life they wish were not so hard, but which at the least they hope will continue to present many options to livelihood in a time of uncertainty and change. A colleague of mine has used the phrase "strategic flexibility" to refer to a rather similar attitude and approach towards livelihood on the part of West Indian migrant workers (Carnegie, 1982). The phrase referred in the West Indian discussion both to a particular pattern of observed behavior and to a set of expressed values or preferences. In the realm of behavior it described both a pattern of rapid adjustment to whatever economic opportunities happen to come along, as well as to the active building of options through establishment of relationships with many new people, through the picking up of odd skills here and there, the constant gathering of information from diverse sources regarding employment opportunities near and far—options which might serve as a hedge against future and chronic job insecurity. As a set of expressed preferences, "strategic flexibility" referred to something which people apparently talked about quite explicitly in many different contexts of Caribbean life.

On both scores—behavioral and expressive—the phrase "strategic flexibility" captures something of Maya livelihood in the forest as well. The be-

havioral aspects have already been mentioned—the changing parameters of slash-and-burn corn farming; the rise and fall of irrigation units; house gardens tended one year, neglected the next. To these can be added the reappearance of collective hunting parties which had in the late 1970's virtually disappeared altogether; the at least temporary shunning of decades-old practices related to the gathering of chicle (now that the market is closed to many in the villages); the chance appearance and pursuit, for several months now and then, of wage labor for any and all takers in local road construction, projects which once completed move on to other parts of the state. Even cattle raising on a very small scale is coming back after a thirty-year absence in many communities. The employment and production picture in the region of this study is, in a word, ever changing. And it has been that way for about as long as anyone can remember. Almost as long, that is; for Mayas' remembrance of the past conditions of laboring and livelihood is detailed and also very relevant to their decisions concerning and their attitudes toward new labor opportunities in the present.

Oral History of Laboring

Mayas in the region of this study—as well as those beyond it, I fully expect—have much to say about the changing conditions of their lives as a laboring people. On a virtually daily basis they exchange information on market conditions in town, on the weather, on movements of game and the luck of hunters in different parts of the forest, on employment opportunities and the latest goings-on in the various government sponsored development projects of their respective communities. This and other talk concerning the daily ebb and flow of opportunity and adversity takes place on street corners, in stores and marketplace, on the bus, and in many other mundane settings of everyday life. In addition to this sort of talk, however, there is talk of another kind and a different relevance: talk of the time of slavery passed, of the lives of servile laborers on nineteenth- and early twentieth-century Yucatecan estates; and talk of the time of slavery to come again, next time in a modern guise.

The oral tradition of slavery among Yucatec Maya is rich and varied. In stories of that time Mayas recall the conditions of servitude under which their distant predecessors labored. A few today are old enough to have seen the final days of slavery; many more knew people who had been slaves, and learned from them what it was like. So people today can describe in considerable detail the schedules and tasks of a slave's workday, for example: two o'clock in the morning one is awakened to rasp leaves of henequen, to extract from them the fibers that will later be made into twine and rope; then it's off to water the master's crib or platform gardens just as the sun is coming up; when that is done, a day's labor in the cornfields begins. In the evening there are still other tasks and just a little sleep before the next two o'clock call that starts the next day's tasks. Failure to perform the assigned tasks—to rasp the standard quantity of henequen, or work the proper extension of cornfield, and so forth—resulted in beatings and in extra labors the following day. Or so, at least, goes the oral tradition of slavery today.

Debt was the basis of such servitude, they say. One couldn't avoid incurring it; and once incurred, one could never get out from under it. A fellow from

one village in the region of my study described how it worked in these words (repeating, he said, what his grandmother had told him many years earlier): One made cornfields back then just like now,

> "But the thing was,
> everything you planted like that, if you wanted to eat it, it couldn't be eaten just like that.
> You would tell your master how much (you had taken).
> You want to eat a couple of yucca roots, you eat them, it's the same story. 'Go ahead, boy, eat them! Eat them!'
> He (the master) grabs his booklet. *Harat harat.* He scribbles it down, the corresponding price. There's no way out for you.
> You are a slave.
> If you want to eat squash or anything, you tell your master.
> 'Eat it, boy!' He won't tell you not to eat it. 'Eat it!'
> He grabs his booklet. *Harat harat.* He's scribbling it down.
> You'll never get out of it.
> You are a slave."

Conversations like that from which the above fragment was exerpted may go on still further, to elaborate other details of slavery as it was: the servile labor of women, the hunger from which many suffered, suicide and flight and the war which slavery provoked, they say—the War of the Castes, that is. And such conversations shade easily into talk of present forms of laboring and indebtedness, as Mayas today speak of the return of slavery prophesied long ago and manifest already in the present.

Whether we consider Mayas of central Quintana Roo as at all justified in speaking of contemporary developments in terms of the prophesied return of slavery is quite beside the point. Even as, for purposes of this discussion, it is irrelevant whether their historical recollections of the nature of nineteenth-century laboring are precisely accurate, so too it is irrelevant whether reasonable people would or could find elements of servility or compulsion behind present-day work patterns. Rather what is relevant is simply that people there *do* talk of slavery, they find it in the changing conditions of their lives both as laborers and consumers, and they will act, if possible, to avoid it.

When these Mayas talk about the return of servile labor they are talking principally about this: They work long hard days, longer and more difficult labor than they recall was customary in times only recently passed, and they get so little for it. Inflation (running during the final period of this study at three hundred percent) is one manifestation, they say, of the return of slavery; indebtedness to government agencies and banks, debts incurred through programs of economic and agricultural development, is another. Unremunerated labor on public works, required of all adult males in Maya communities, is yet another. Corporal punishment was once the hallmark of a slave's bondage; but it has no place in the new. No, they say, the matter has been "studied", and slavery will come in a new form, probably based principally upon the manipulation of the supply and price of commodities. Yet the effect will be the same, particularly for those working on projects where they earn a wage rather than a share of the produce or the proceeds from the sale of the produce; or where their indebtedness to banks is greatest, as in cattle-raising cooperatives. Sooner or later, they say, someone begins to tell you where and when to work, and fixes what the returns to you will be. There

was a kind of security, they recall, in the livelihood of a slave of the past. The master provided food and clothing and shelter, yes. So the provision of the same today, the achievement of a kind of security as a ward of the government or a laborer on a government-managed project, does not obviate comparisions to the time of slavery—on the contrary, it makes such comparison seem all the more true. The condition of laboring is the index of slavery and freedom; not full or empty bellies.

Now it may seem that the discussion here has strayed quite far from the main topic of this paper—agricultural change in central Quintana Roo—into the realm of other peoples' idle-time talk. But the talk and the remembrance of the laboring conditions from which their predecessors escaped at great cost in lives and suffering does have bearing upon how Mayas of central Quintana Roo today live and labor in the forest.

First, they consciously seek to avoid involvements which might seriously limit their future options as laborers. Some groups have been formed in Maya communities for the purpose of raising cattle—cutting down swaths of the forest, planting them in grasses, and purchasing cattle, activities which entail heavy outlays of borrowed capital. But such activities are much criticized and shunned in other communities where it seems to people that such involvement turns cultivators into employees of this bank or that. Some of the critics themselves raise cattle, by the way—but a few head or a few dozen head on ranches which are devoted to a multiplicity of other productive uses as well.

In some communities Mayas have been reluctant to accept much-offered bank credit to finance expansion of acreage under cultivation in corn, acreage cultivated by traditional slash-and-burn techniques. In the community of Tuzik a third or so of the village men did eventually enlist in such a scheme, but only years after their neighbors had tried it and after they themselves had overcome expressed fears of debt servitude. And after all of that, it was only for one year—a year when they happened to really need the money.

Secondly, Mayas consciously seek to maximize options, much like their West Indian counterparts for whom the phrase "strategic flexibility" was coined. Most send their children to school, some to trade schools at the secondary level. And the adults seek to learn as well new cultivation techniques for both rain-fed and irrigated agriculture. While multihousehold production units of the type promoted by the government come and go over the years, there is something quite tangible which remains and which needs to be considered when evaluating the impact of such projects. Ewell, writing about farmers in the Puuc Hills region of Yucatan, talked of the slow and deliberate accretion of equity by farmers who engaged in irrigated cultivation while remaining independent, to a great extent, of government projects dedicated to the same. The equity of which Ewell wrote was in the acquisition of parcels of irrigated land, the extension of irrigation canals, the introduction of improved varieties of fruit trees, and more. Infrastructure, in other words. Still independent cultivators in central Quintana Roo are far from developing equity of that sort. Perhaps it is simply to early to detect in this period of introduction of and experimentation with new modes of agricultural production. Perhaps things will never move in that direction for many reasons. In any event there is still a kind of accumulation of equity insofar as there is accumulation of knowledge—

knowledge which creates options for each year's disposition of labor.

While the government-sponsored projects come and go, what is learned in those projects is applied in the houselot, or in the single household garden on the village periphery or near water sources in the forest. The techniques are practiced there and so preserved. They are preserved in that same oral tradition that retains in such detail knowledge of the workday of a slave, or which recounts the rudimentary but ingenious technology of a war which their grandparents and great-grandparents fought. Mayas of this region have been learning also over the last five to ten years how to claim what they now consider their right to technical and financial assistance from a government which not long ago they considered quite foreign and predatory. How to form a credit group, how to write petitions, who to talk to for assistance, and how to talk to agronomists and other project personnel, what the relationship might be between their demonstrable labors in the field and the actions of agency directors in the towns—these are all part of the new experience of Maya cultivators in the forests of Quintana Roo, accumulated experiences which from season to season they can put to use in various ways. Press (1975:44-70) makes some very similar observations concerning a town in Yucatan, phrasing them in terms of the general theme of continuity with change.

Freedom and the Forest

There are constraints to Maya flexibility in the uses of their labor, of course, and this brings us to the final point of this paper. Assuming that Mayas of central Quintana Roo (and, it seems, of other parts of the peninsula) value flexibility in the disposal of their labor and of the products of their labor, assuming that they actively cultivate such flexibility in a changing environment, within what limits can such "strategic flexibility" function successfully or effectively? What are the preconditions for the achievement of such flexibility? Mayas themselves have commented upon some—avoid severe indebtedness of the sort which turns control of the production process, and of one's labor in particular, over to others more powerful and rich than oneself. But there are other constraints. One concerns the scale of the production options which Mayas alternatively deploy or abandon; and the other concerns the nature, the integrity, of the forest in which they live and labor.

Each of the various production alternatives which this paper has discussed are deployed on very, very modest scales in central Quintana Roo. The largest of the multihousehold irrigation units is twenty acres; that is towards the upper range of a single household's corn acreage for a single year. The capital investment in such projects is quite small, compared to comparable developments in cattle raising, for example. The infrastructure is modest as well. And the cultivation techniques involved in such multihousehold units are also to some extent transferable and applicable to houselot or single household irrigated cultivation. With his experience in one such project, a fellow goes home and plants watermelons which he irrigates and fertilizes in the manner he was taught at the project site; another fellow opts for chile, planting in his houselot enough bushes to make a trip to market with the produce once a week. And so on and so forth. Irrigation units much greater in size or with very different organization and

technique might well pose more severe limits to the sort of flexibility I have been describing in this paper, it is true. But for the time being, at least, government projects in Quintana Roo have provided participants with techniques and knowledge that serves them as a kind of equity deployable in other and future endeavors.

Finally, for all of the households in this region, slash-and-burn corn farming remains the basis of household economy and the mainstay of sustenance. Destroy the forest and the household too would crumble. Where then will people get corn? What about game, the income from their apiaries, fuel for the household kitchen, and even fertile soil in which to conduct modest degrees of intensive cultivation? Should the forest sources of these and other elements of Maya livelihood be lost—whether through changes in the way Mayas labor in the forest, or through other factors largely beyond their control—then these Mayas would truely become dependent upon that marketplace and labor market whose effects upon their freedom they so suspect (Alonso, 1979).

Mayas of central Quintana Roo, either alone or with the assistance of outside agents, will destroy the forest for short run gain, to make a living now, without regard to future needs and the security of the next generation. They will, and to some extent are, doing that. But they would be amenable to preserving the forest as well, just as they fought for decades to preserve their access to it in time of war and in time of peace. They will do so because the freedom they so value (and the return of slavery they so fear) are intimately linked with the nature and existence of the forest. What they seek right now are options to livelihood and flexibility in laboring, options which they evaluate not only on the basis of short run returns, but in terms of the multiple ramifications they have upon the quality of life and the preservation of freedom.

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Mesoamerica's Tropical Rainforests
Conflicts and Conservation

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One hundred years from now, the second half of the 20th century will be known as that brief period of time when much of the earth's biological diversity was eradicated in the name of survival, progress, and profits. Paleontologists speak of the end of the dinosaur age as a period of massive extinctions, yet during that period—despite the assistance of asteroids and dust clouds—the planet lost an average of only one species every 1,000 years (Simberloff 1982). Today, human activities are eradicating plant and animal species at the rate of 1,000 per year. By the end of the century, this rate is expected to reach 10,000 species per year, or more than one per hour (Myers 1979a; Ehrlich and Ehrlich 1981; Wilson 1984:13).

If this prediction sounds unbelievable, keep in mind that these figures are not the armchair ruminations of outraged conservationists. They are the accepted estimates of some of the world's most eminent biological researchers. If their predictions hold true, by the time we finally make peace with our planet, our activities may have destroyed one-quarter of all the species of animals and plants that live on earth today (Barney 1980, 1:3).

Most of the species being eradicated are insects—chiefly beetles and butterflies—and most of them are restricted to small territories. But they are joined by a variety of birds, mammals, and reptiles, and by thousands of species of plants. The primary cause of this massive eradication of species can be defined in one phrase—loss of habitat. In turn, that phrase can be narrowed down to one word, deforestation, chiefly of the world's tropical rainforests, the areas we commonly think of as "jungles."

The reason that tropical forest destruction is so severe is simple: they are the world's largest depository of plant and animal species. Tropical forests are home to more than half of all the species on earth (NRC 1980:35; Ehrlich and Ehrlich 1981:159; OTA 1984; Myers 1984:50).

The ironic thing about this destruction is that we know very little about what we are destroying. Five out of six tropical species have never been seen by scientists. That amounts to at least two and one-half million unknown species, or about twice as many as taxonomists have described and named since Linnaeus began the process 230 years ago (Raven 1981:30). We're only now beginning to realize the potential that rainforest species hold for the well-being of humankind. Forty years ago, for example, the yam of the Mexican barbasco vine (*Dioscorea composita*) was known only as the source of a fish poison used by rainforest Indians to stun fish in rivers. Then, in the late 1930s, a chemistry professor, Russell Marker, gathered the plant in the rainforest of southeastern Mexico and isolated a steroid called diosgenin, which today is the active ingredient in oral contraceptives. Around the world, 80 million women now take oral contraceptives, and the barbasco vine has become the basis for a prosperous industry in Mexico (Myers 1979b:5; Djerassi 1984:127).

That's one minor example of the positive potential that hides in tropical rainforests, because rainforests are a liv-

ing chemical factory that we've only begun to examine (Schultes 179:264). So, when we say that during the next 20 years, human activities will destroy hundreds of thousands of species of plants and animals in these forests, how many new medicines, new food crops, natural insecticides, and oil-producing trees are we destroying? The answer is that we don't know. All we do know is that tropical rainforests and the species that live in them are being effectively eradicated in many of the world's tropical countries.

This is not to say that rainforests are doomed to disappear. The forests in some areas of the world are not yet in danger. In Africa, the rainforests of Zaire and Gabon should survive for many decades. And in South America, the rainforests of Guyana, Suriname, French Guiana, and of much of the western Brazilian Amazon should stand for at least another 50 years (NRC 1980; Raven 1981:30).

But things are not that bright throughout the rest of Latin America. In the eastern and central sections of the Amazon Basin, bulldozing, burning, and chemical defoliation wipe out huge areas of forest every dry season (Barrett 1980; Goodland 1980; Fearnside 1982). The situation in Mesoamerica—Mexico, Central America, and Panama—is the most alarming anywhere in Latin America. More than two-thirds of the region's original tropical broad-leaved forest have been cleared and burned, mostly during the past 40 years (Nations and Komer 1983a:232). Mesoamerica's tropical forest once stretched from Veracruz, Mexico to the Darién of eastern Panama. Today, only three large blocks of rainforest remain: (1) around 40,000 km^2 in the Guatemalan Petén and its adjacent flanks—the rainforest of southern Belize and the *selva Lacandona* of Chiapas, Mexico; (2) approximately 46,000 km^2 along the Miskito Coast of eastern Honduras and Nicaragua; and (3) about 21,000 km^2 in the Darién province of southern Panama. At current rates of clearing and burning in the region, the final third of Mesoamerica's tropical rainforest will be eliminated within 20 years, leaving only degraded remnants in parks and forest reserves. In sum, Mesoamerica is one of the most threatened tropical forest regions in the world.

These statistics lead us to ask some simple questions: Why should we care? What good are Mesoamerica's rainforests anyway? The answer is that the consequences of rainforest destruction are more severe than just the extinction of beautiful birds, new drugs, and new food plants. Rainforest clearing has repercussions on all sorts of human activities.

On a local level, destroying rainforest can increase flooding, cause soil erosion, and lead to the siltation of lakes and rivers. Rainforests normally act like a giant sponge; they absorb and recycle the precipitation that falls on them. If the forest is cleared, the torrential rains of the tropics hit the soil, run down the slope, and carry the soil with it. The result is increased flooding because there is no vegetation to absorb the rain, and massive soil erosion because the run-off carries the soil with it (Gentry and López-Parodi 1980; Myers 1984:261). Because the forest protects the soil from rain and run-off, one hectare (2.471 acres) of standing rainforest will lose only one kilogram of topsoil per year due to erosion. But when cleared of forest, that same hectare of land can lose up to 34 tons of topsoil (Goodland and Irwin 1975; Sanchez 1976; Tirado and Lugo-López 1984).

Downstream, this lost topsoil be-

comes silt that can wipe out fish populations, damage crops, and produce a variety of economic and ecological consequences for people who live from farming or fishing (Barrett 1980:215; Lovejoy 1973; Smith 1982; Goulding 1980; Bunker 1980:36-37). On a national level, this same siltation can cut the lifespan of hydroelectric projects in half by filling in the lakes that provide water used to generate electricity and irrigate agricultural land (Szekely 1976; Goodland 1979; Caufield 1982). Siltation caused by deforestation of the watershed that feeds the Panama Canal is producing topsoil accumulations up to 22 feet deep in Lake Alajuela, and dredging operations already close the canal for days at a time (Isaza and Moran 1981; USDA-AID 1980:68). Some researchers predict that by the time the Canal is fully transferred to Panama in 1999, it may have become a worthless ditch—with all sorts of consequences for Panama and for international trade (Wadsworth 1978:23).

Deforestation also changes microclimatic conditions by causing more extreme fluctuations in surface temperature, making cultivation areas hotter by day and colder by night (U.S. Interagency Task Force 1980:19). And, more seriously, tropical forest destruction can cause a decline in the amount of rain that falls. Studies in Panama and in the Amazon show that over half of the rain that falls on a tropical forest is water derived from the forest itself. The leaves of forest vegetation breathe out water vapor that is equivalent to thousands of gallons of water per acre per day. When the forest is cleared, that recycling system is destroyed, and the amount of rainfall can be cut in half, as it already has been in some deforested areas of Panama and Brazil (Salati, Marques, and Molion 1978; Barrett 1980:215; Leopoldo, Franken, and Matsui 1984; Myers 1984:280).

Deforestation is also leading to the loss of one of the most important resources in the tropics—the indigenous people who have made the forest their home for thousands of years. The loss of these groups is tragic—not just because they are losing their traditions and their lives—but also because you and I are losing the knowledge that these groups have developed and refined about our planet's most complex ecosystem.

Without a doubt, tropical forest peoples are the world's foremost tropical ecologists. No team of scientific researchers can match the knowledge of the rainforest that is controlled by an Amazon Indian or by a Lacandon Maya Indian. Like the case of eradicated species, we still don't know what we're losing when these people are pushed off their land by mining operations or cattle ranching or when they die from diseases introduced by road construction and logging teams.

We're only beginning to have some indication of the information that rainforest peoples could share with us, if we had time to collect that information. The list of what they've already given us is impressive. As an example: among the tropical forest plants that indigenous people have introduced us to are cacao for chocolate, brazil nuts, sweet potatoes, tobacco, avocados, vanilla, coffee, manioc, mangos, papaya, peanuts, cinnamon, bananas, and sugarcane (Myers 1979a:122; NRC 1980:44; Barrett 1980:216; Schultes 1979). Just one of these crops, manioc—which we know in the United States mainly in the form of tapioca—is the dietary staple for 300 million people in Africa and South America (Cock 1979:186; Schultes 1979:259).

We've also learned to use other materials from tropical forest peoples—materials like rubber, gum arabic for ink, pharmaceuticals, the glue for postage stamps, latexes for chewing gum and golf balls, and, again, human contraceptives. Rainforest tribes in South America have already led researchers to 268 different plants that can be used to control human fertility (Moreno Azorero and Schvartzman 1975). As the world's rainforest peoples are wiped out, this knowledge of the rainforest is also eradicated. So, in addition to being the brief period of history when much of the earth's biological diversity was eradicated, the second half of the 20th century will also be known as the period when we witnessed the disappearance or dispersal of people who knew the most about this biological diversity.

All of this information begs the question: If rainforests are so important, why are they being destroyed in the first place? In Mesoamerica, the causes of tropical forest destruction can be narrowed down to three stages.

The first stage is road construction. The outside world literally bulldozes its way into Mesoamerican rainforests in the form of road construction. Rainforest roads are built for a variety of reasons. Oil exploration and military control are two increasingly important reasons, but in most cases, rainforest roads in Mesoamerica are built for logging. Logging teams build roads to penetrate the rainforest and take out commercially valuable timber. In Mexico and Central America, this means mahogany and tropical cedar that ends up on the international market for use as office paneling, in boats, and as fine furniture.

To get these trees, tropical loggers carry out what they call "creaming" or "highgrading" the forest. Because tropical forests bear such an incredible diversity of plant life, you may find 200 different tree species on a one hectare plot (Whitmore 1980:309; Myers 1984:26). That means that you'll find only a few single individuals of any particular tree in any particular area. So loggers bulldoze roads through the forest, then spread feeder roads out from these major roads and send long drag lines to pull out the few trees per hectare that are commercially valuable.

You can predict that this process will destroy a certain amount of forest. Rainforest trees are tied to one another at the crown through an interconnected mass of vines and vegetation. So, when loggers pull down one mahogany tree, surrounding trees come down with it. Also, as that tree falls, it may wipe out trees that it lands on. In sum, felling a single commercially-valuable tree can cause the destruction of an average of 17 non-commercial trees (Ng 1982). Considering this and the areas cleared for roads, staging areas, and stacking areas, logging operations may end up destroying 30 percent of a forest where only a few trees per hectare are extracted (Whitmore 1980:311; Ranjitsinh 1979:193).

The problem with logging, though, is not so much what the loggers take out as what they leave behind—namely, the roads that they've built to enter the area. Roads introduce the second stage of rainforest destruction in Mesoamerica: colonization. Landless farm families from other regions of the country, or even from other countries, file down these logging roads and create new jungle settlements, where they clear the forest to raise subsistence crops like corn, beans, and manioc, and cash crops like coffee, cacao, and *chiles*.

This second stage of deforestation has a heavy impact on indigenous popu-

lations that live in the forest. The new immigrants sometimes show little regard for the area's Indian inhabitants. They push them off their traditional land, introduce diseases, and disrupt communities. Colonists also do not share the Indians' knowledge of the rainforest environment. As a result, they may end up destroying vast expanses of forest in trying to make it yield a living.

Some scientists, and many politicians, like to blame colonizing peasant farmers for the destruction of tropical forests in Mesoamerica. But that's like blaming soldiers for causing wars. Peasant farmers do much of the work in clearing and burning tropical forest, but they're simply pawns in a bigger man's game. To understand the role of peasant colonists in tropical forest destruction, we have to ask why they are in the rainforest in the first place. The answer to that question is that there's no land for them anywhere else. There are two reasons behind this situation.

The first reason is Mesoamerica's unequal land tenure system. Peasant families may be forced to colonize forest lands in the lowlands because the farm land that would support them is in the hands of a fraction of the region's population, frequently corporations or families who use it to produce commercial crops for export. In Latin America as a whole, a mere 7 percent of the population controls more than 93 percent of the arable land (Eckholm 1979:11).

In Central America itself, the percentages differ from country to country. In Guatemala, 2 percent of the landowners control 80 percent of the agricultural land, mostly in form of banana plantations, coffee fincas, and cattle ranches. Meanwhile, 83 percent of the rural population either owns no land or lives on plots that are too small to maintain a family (World Bank 1978:12, 19). In Nicaragua, until 1979, one percent of the population owned 50 percent of the farmland; the Somoza family alone controlled 23 percent of the nation's agricultural land (Molina 1980:34; Cultural Survival 1980:9). In El Salvador, 2 percent of the population owns almost all of the nation's fertile land and 57 of total national territory. Most of that land is dedicated to coffee, cotton, cattle, and sugarcane (Arnson 1980:2; LaFeber 1983:10, 252). Gross inequality of land ownership also characterizes Honduras, where five percent of the landholdings account for 60 percent of the nation's cultivated land (U.S. AID-Honduras 1982:37). Even in Costa Rica, the country considered to have the most equitable economic structure in Central America, three percent of the population owns 54 percent of the farm land (U.S. AID-Costa Rica 1982:6, 65).

In sum, one-half of the rural families in Mesoamerica either own no land or own too little to support a family (Eckholm 1979:9; Lassen 1980). To support themselves, these families serve as day laborers harvesting coffee, picking cotton, or cutting sugarcane. Or, if they're lucky, they eventually migrate to the rainforest to claim their own plot of land.

They do this both legally and illegally. Governments sometimes promote the colonization of rainforest areas because doing so temporarily defuses demands for land reform in other areas of the country (Eckholm 1979:29; Leonard 1985:102, 169). In a related move, governments may also promote colonization to demonstrate sovereignty over areas that are populated only by Indians. In South America, this has happened in Brazil, Venezuela, and Colombia. In Mesoamerica, it has taken place in Costa Rica and especially along

the border of Mexico and Guatemala. This is the oil-rich region of the Chiapas-Guatemala border, and each country accuses the other of trying to steal its oil. In Guatemala, the combination of government-sponsored colonization and the need to establish sovereignty led to the resettlement program of the Franja Transversal del Norte. Across the border in Chiapas, these same forces are leading to the colonization of the last remaining rainforest in Mexico, an area called the Marques de Comillas, where thousands of peasant colonists are now being settled to raise corn and cattle (Plan Chiapas 1983).

The second major factor that brings colonists into the rainforest is population growth. Overall, Mesoamerica's population is growing as fast as Africa's. The region has an average rate of increase of 2.9 percent per year, giving it a doubling time of 24 years (Leonard 1985; Latin American Times 1984:24). Over the next 20 years, more than 90 percent of Mesoamerica's population growth will take place in areas that are covered by rainforest or were formerly covered by rainforest (Teller 1981; Teller et al. 1979). It seems obvious, then, that even a massive redistribution of land in Mesoamerica will not be able to provide future generations of farmers with sufficient land as long as population growth remains that high. We can also assume that as long as there is rainforest land left to colonize, landless families will continue to migrate into those forests and clear it to support their families. For the majority of Mesoamericans, this is the only way they'll ever be able to own their own land.

No matter why it takes place, colonization in Mesoamerica consistently leads to a third and final stage of tropical deforestation. This is the expansion of commercial export crops into the rainforest, and this is basically the driving force behind deforestation. During this final stage, land that has been cleared by colonists is absorbed by a second wave of landowners who follow behind the pioneer front, buying up small landholdings to combine them into large plantations for the production of export crops. In Mesoamerica, the most dominant and most destructive of these export crops is beef cattle (Parsons 1976:126; DPN 1978,II:B-55; Nations and Komer 1983a, 1983b).

Cattlemen obtain the land of colonist families in a variety of ways. Farm families may willingly sell the land they've cleared when weeds, insects, and declining fertility overpower their hand-labor farming methods. Because they don't have money for fertilizers and because no extension agents are on the spot to teach them how to raise crops on a sustained-yield basis, they sell their land to the cattlemen and move on to clear new forest. In some areas of Mesoamerica, cattlemen themselves buy tropical forest land and allow colonists to settle on it. The colonists get the right to clear the forest and plant crops in exchange for leaving the cleared land planted in pasture two or three years later (Merkel 1981; CIES 1979).

In other cases, colonization and cattle production are combined. In the Darién region of southern Panama, for example, colonists settle on national land, clear it, and burn it, and then sell it for $80 a hectare to week-end cattle ranchers from Panama City. These new landowners aren't interested in producing cattle as much as they're interested in holding onto the land as a hedge against inflation (Chapin 1980; Heckadon 1981; Raven 1980; cf. Fearnside 1983:143).

Colonizing families also get involved in the rainforest cattle industry. They sometimes find that they can obtain bank loans to produce cattle, but not to raise corn and beans. So, they clear the land, raise calves, and sell these calves to ranchers who fatten them and sell them on national or international markets. The way grain prices are structured, a family can make more money raising two and a half calves per year than they can raising food such as corn and beans (Price and Hall 1983:44-46).

No matter how the land is originally cleared, the end result is the same. After seven to ten years of mediocre beef yields, erosion, weeds, and loss of fertility prompt the cattlemen to search for new pasturelands (Fearnside 1979, 1980, 1983). They move farther into the forest and clear more land, and repeat the cycle until the forest is gone. This has already happened in El Salvador, and is happening fast in Chiapas, Honduras, Guatemala, Nicaragua, Costa Rica, and Panama (Nations and Komer 1983a:15).

The tragedy of the process of converting rainforest to pasture is apparent on several levels. First is the pathetic yield that cattle ranching produces on cleared rainforest land. The average stocking rate on cleared Mesoamerican rainforest lands is one head of cattle for every 1.6 hectares of pasture. The average yield is approximately 10 kilograms of beef per hectare [9 pounds of beef per acre] (Duayhe 1979; Myers 1981; Price and Hall 1983; Redclift 1981:233). Just as a comparison, on the same amount of land and without permanently destroying the rainforest, a Lacandon Maya farmer can produce six tons of shelled corn per hectare, and another several tons of root crops and tree crops (Nations and Nigh 1980). Yet cattle production is replacing the Lacandon Maya farming system because it's tied into the national economy, the banking system, and land speculation.

Transforming forest into cattle pasture also fails to aid the colonists who live in rainforest cattle areas. In the first place, raising cattle requires less labor than most other production systems, so few jobs are created (Tosi 1972:8; Fearnside 1983:75; Price and Hall 1983). In southeastern Mexico, tropical cattle ranching requires an average of only one worker per 100 hectares of pasture (Romanini 1978:4). "The International Labor Office estimates that cattle raising requires only six worker-days per hectare, while rice needs 60, beans 37, potatoes 120, and coffee 130" (CEPAL, 1980:175, cited in ICAS 1982:10). But more important is the fact that the beef produced on this land is exported out of the area, either to the middle class consumers in Mesoamerican cities or to other countries.

Two-thirds of Central America's farm land is now devoted to livestock production rather than to producing food for the region's expanding population (Parsons 1976:124). In Costa Rica alone, 82 percent of the productive land is now in pasture (ICAS 1982:10). In the selva Lacandona of Chiapas, Mexico, more than 80 percent of the land cleared from rainforest is dedicated to cattle pasture (Lobato 1981:21). Despite this huge investment of land in beef cattle production, Mesoamerica's per capita beef consumption is only 13.7 kilograms per year (Nations and Komer 1983a). By contrast, here in the United States, we eat three times that much, and our house cats eat more beef in a year than most individuals in Mexico and Cental America.

Meanwhile, beef production continues, and rainforests continue to fall, because beef production is concentrated

in the hands of a small percentage of the population. This group is making good profits, and they will continue production as long as the market holds up, even if it's at the expense of rural families and tropical forests.

Mesoamerican cattlemen have several incentives to expand their production into the rainforests. In the first place, they have a lucrative foreign market for the beef they produce. Unfortunately, because cattlemen are able to sell their beef internationally at a good price, the local price of beef frequently rises beyond the reach of many Mexicans and Central American families, so that only the urban middle-class can afford a steak dinner.

The lucrative foreign market means income for the individuals who own beef cattle lands, and it means income for the Mesoamerican nations as a whole. The fact that there is money to be made attracts commercial bank loans and international assistance (Sims 1961:10). The World Bank and the Inter-American Development Bank have provided loans to expand the cattle industry in every Central American nation except El Salvador (Shane 1980). The Organization of American States, the Pan American Health Organization, the U.S. Agency for International Development, and the U.S. Department of Agriculture provide technical assistance to control cattle pests such as ticks, vampire bats, screwworms, and hoof and mouth disease (Rourk 1969; Nelson 1973). All of this financial and technical assistance is geared to the fact that, along with coffee, cotton, bananas, and sugar, beef is now one of the major

TABLE 1. Central American beef production, consumption, and exports 1959–1984 [in thousand metric tons, carcass weight (with bones)].

Date	Production	Consumption	Total Exports	Percent Exported
1959	124	113	11	9
1960	130	111	18	14
1961	145	125	21	15
1962	145	113	31	21
1963	152	110	42	28
1964	154	115	39	25
1965	170	136	35	21
1966	156	111	46	29
1967	167	109	59	35
1968	183	115	68	37
1969	233	148	86	37
1970	252	136	116	46
1971	282	177	107	38
1972	292	162	131	45
1973	281	161	121	43
1974	285	167	118	41
1975	297	178	119	40
1976	330	194	137	42
1977	339	210	129	38
1978	391	236	152	39
1979	400	240	163	41
1980	355	246	110	31
1981	355	254	101	28
1982	353	262	91	26
1983	336	257	79	24
1984	341	261	80	23

Source: various documents, USDA Foreign Agriculture Service.

TABLE 2. Mexican beef production, consumption, and exports 1960–1984 [in thousand metric tons, carcass weight (with bones)].

Date	Production	Consumption	Total Exports	Percent Exported
1960	354			
1961	375	339.3	35.7	9.52
1962	396	357.5	38.6	9.75
1963	428	381.8	46.2	10.79
1964	440	407.7	32.3	7.34
1965	463	432.2	31.0	6.70
1966	469	430.5	38.8	8.27
1967	474	444.3	30.2	6.37
1968	500	454.6	45.7	9.14
1969	534	485.2	49.5	9.27
1970	590	538.8	52.1	8.83
1971	581	532.9	48.6	8.36
1972	592	534.2	58.3	9.85
1973	744	706.1	38.5	5.17
1974	844	824.7	19.6	2.32
1975	889	875.4	14	1.57
1976	986	963.3	23.3	2.36
1977	1,040	1,011.0	30.1	2.89
1978	1,054	1,010.0	29.7	2.82
1979	946	948.0	6	0.63
1980	1,065	1,065.0	1	0.09
1981	1,129	1,137.0	1	0.09
1982	1,200	1,201.0	0	0.00
1983	975	969.0	8	0.82
1984	1,060	1,036.0	25	2.36

Source: various documents, USDA Foreign Agriculture Service.

foreign exchange earners for the Central American nations.

The next question is who is purchasing all this beef? The answer is very close to home. Ninety-five percent of Central America's beef exports go to the United States. Despite periodic cut-offs, U.S. companies buy and import between one-fourth and one-third of all the beef produced in Central America. During 1984, we imported 176 million pounds of Central American beef—one-fourth of all the beef the region produced. That doesn't count the live cattle we imported from Mexico for fattening in Texas feedlots. Incidentally, the role of beef exports in rainforest destruction in Mexico is a bit more indirect. There, the beef raised on cleared rainforest land goes to Mexico City, while the cattle raised in the more arid, northern states of Mexico are those exported—frequently on the hoof—to the United States (Yates 1981:91, 97).

The next question is why would the United States—which is already the world's largest consumer and producer of beef—need to buy more beef from Mesoamerica? The answer to that question is hidden in the dramatic rise of the American fast-food industry. During the 1960s, cattlemen in the United States took advantage of the availability of cheap feed grains like corn and sorghum and began producing grain-fed cattle, which produce higher profits than grass-fed beef (Koch and Algeo 1983). As domestic cattlemen switched to producing the finer cuts of beef, U.S. companies had to look elsewhere to find sources of what they call "canner" and "cutter" grades of meat.

That move by U.S. cattle producers coincided with the blossoming of the

U.S. fast-food industry, which, in turn, was put into motion by various other changes in American society. The U.S. now has 53,000 fast-food restaurants, and we eat one-third of our meals outside the home. Within five years, we're expected to be eating one-half of our meals away from home. Many of these meals are based on beef, and much of that beef is of the lean, lower-grade type which is raised on grass, not grains (Nations and Komer 1983a:18).

To meet the new demand for cheaper cuts of beef during the 1960s, the U.S. increased its beef imports from Australia & New Zealand, Ireland, Dominican Republic, and Haiti, and it is important to point out that these countries still supply 75 percent of our beef imports. But U.S. beef importers added Central America to its sources because of its proximity, and because the area is free of hoof-and-mouth disease. U.S. law prohibits beef imports from countries infected with hoof-and-mouth disease. The fact that South America is infected with this disease has helped keep the Amazon rainforest from being turned into a cattle ranch for the United States. We do import cooked and canned beef from South America, but no fresh or frozen beef. Instead, South America exports beef to Western Europe, which is also infected with hoof-and-mouth disease (Simpson 1981:13; Simpson and Farris 1982).

The beef imported into the U.S. from Central America arrives on refrigerated ships of the Coordinated Caribbean Transport or Pan American Shipping Line, loaded in piggy-back, refrigerated trailers. It is unloaded in Miami, Philadelphia, and New York, where it's purchased by beef brokers and packing plants. These middle men sell it to other meat product manufacturers and to fast-food restaurants. Most of it goes into luncheon meats, frankfurters, chili, beef stew, soups, sausages, t.v. dinners, baby foods, and pet foods, but some of it is mixed with fatter, U.S. produced beef and ends up as ground meat on supermarket shelves (Nations and Komer 1983a).

Some of the fast-food restaurants admit that they use imported beef: Burger King, A & W Root Beer, Jack-in-the-Box, Roy Rogers, for example. Others, notably McDonald's and Wendy's, apparently don't (Shane 1980; Nations and Komer 1983a). But there are problems in determining what's imported beef and what isn't. Once it's been inspected by U.S. Department of Agriculture officials at the port of entry, foreign beef is no longer required to be labeled "imported." It simply becomes another grade of U.S. domestic beef. So some fast-food franchises can claim that they use only domestic beef in their products and be accurate, though not truthful.

I want to stress that the problem of rainforest destruction for beef production does not revolve solely around the U.S. fast-food industry. The U.S. market for imported beef helped push the Central American cattle industry into rainforest areas, but the problem is now larger than that. In fact, U.S. imports of Mesoamerican beef are actually declining, mostly in reaction to increased concerns about the health implications of a diet rich in red meat (This Week 1982:239). But beef *production* is only slightly down in Mesoamerica, and beef consumption is higher than it has ever been. Today, most of the beef produced in Mesoamerica is consumed in Mesoamerica.

It is important to point out again, though, how unevenly that beef consumption is spread around. The urban middle-class in Panama City,

Tegucigalpa, and San José, Costa Rica eats a great deal of beef now, including Big Macs and Super-Gigante *hamburguesas*, but the rural farm families who make up over half of Central America's population are not benefiting from this industry. Instead, they are continuing to scratch out a meager living in an increasingly degraded environment, and they are continuing to expand in number.

Now, what would you predict, if you looked at an area where the majority of the farm land is in the hands of a wealthy elite and large corporations, where export production is increasing, per capita food production is declining, where the ecosystem is being severely degraded, and where the population is doubling every 24 years? What you get is Mesoamerica and the economic, nutritional, and political battles that the region is involved in today.

So what can we do about it short of sending in the troops and trying to maintain the status quo? The answer is not to ban beef imports from Mexico and Central America and hope that the rainforest grows back. That's not going to happen. What we can do, though, is expand research on intensifying production on the land that's already been cleared. Studies have already shown that beef production in Latin America could be increased 10 times without clearing another tree (Parsons 1976). Systems like rotational grazing systems, improved breeding, and forage feeding can produce higher yields of beef without degrading the environment and without destroying the national income that results from selling beef. But the practice of clearing tropical forest to raise beef for seven to ten years and then abandoning the land to weeds and erosion has got to be eliminated.

Just for starters, we can work toward ending international subsidies for beef production in rainforest areas. Despite their claims to the contrary, the World Bank and Inter-American Development Bank are still paying for forest clearing to produce cattle (World Bank 1983:25; World Bank 1984:122; Leonard 1985:412 ff.). There are positive steps happening on that front, though. Environmental groups like the Natural Resources Defense Council and the National Wildlife Federation have banded together to work toward coercing these development banks into putting stricter environmental reviews into their loan precedures (Committee on Banking 1984).

An even more important step is to take the money that is now subsidizing beef production and use it instead to intensify food production in Mesoamerica. Our challenge is to improve the lives of rural families by allowing them to increase agricultural production on land that's already cleared. If we hope to preserve any of the region's biological diversity, we have to provide these families with the technical and financial support they need to produce food and cash crops without having to continually clear more forest.

Fortunately, some good progress is also being made toward these goals. One of the most promising techniques is the tropical *chinampa* being developed in Mexico. To create chinampas, the farmer digs narrow trenches on at least three sides of a small cultivation plot in an area where water is available year round—either in a very wet area or near a river or lake. He adds the excavated soil to the plot to elevate and fertilize it, then plants his crops in this mud-rich area. He periodically dredges the mud from the trenches to renew the plot's fertility, so that he can produce food crops, cash crops, and trees year round

without the use of chemical fertilizers or machinery. One plot 2,000 meters square can feed a family of five year round and give them an income to boot (Coe 1964; Gómez-Pompa et al. 1982; Gómez-Pompa 1978; Gómez-Pompa and Venegas 1976; Gliessman et al. 1978).

That's one example of the kind of system that will have to be taken from the experimental stage to wide-scale use if Mesoamerica's population is expected to feed itself without destroying its natural ecosystems. Another good example is agroforestry. This is a system in which the farmer *plants* trees with his crops, rather than clearing the trees in order to plant crops. Some of the best research on agroforestry is being conducted at CATIE in Turrialba, Costa Rica, where foods crops and fuelwood crops are being grown in layers with lumber trees and cash crops such as coffee (CATIE 1979). Incidentally, one of the prime sources of new ideas in agroforestry systems is the traditional agriculture of indigenous populations. The Lacandon Maya, for example, maintain a system of traditional agroforestry that allows them to produce crops on a single plot of cleared rainforest for five to seven years. Then, rather than abandoning the plot, they plant it in tree crops and continue to harvest it as it regrows in natural forest species (Nations and Nigh 1980).

Because agroforestry combines crop production with the advantages of a standing forest, it is one of the main hopes for the tropics. Agroforestry systems can also be combined with cattle production, using forest grazing systems with nitrogen fixing trees such as *Leucaena* (NAS 1977). By expanding intensive agricultural systems like these, and other systems such as aquaculture, we can help rural communities produce higher food yields, help improve their living conditions, and simultaneously work for the conservation of the tropical forest environment. The author's message here is simple: in order to conserve Mesoamerica's tropical forest, we must put most of our emphasis on other issues—issues such as tropical agriculture, international trade, and the financial decisions of national governments and multilateral development banks. The key to tropical forest conservation actually lies outside the rainforest itself.

That's not to say, however, that parks and other conservation units should be neglected. The creation of more and larger national parks must continue concurrently with increased emphasis on countering the trends that threaten tropical forests. Costa Rica deserves recognition for setting the example of how to create a successful system of national parks and forest reserves. Costa Ricans have incorporated 19 percent of their national territory into protection units (U.S. AID-Costa Rica 1982:3; Gonzáles 1979; Nature Conservancy 1984). That's the equivalent of our declaring the state of California a national park.

One of the other positive signs is the Biosphere Program of UNESCO. Biosphere reserves are designed to have an unviolated core of natural vegetation surrounded by concentric rings of land with increasingly more intensive human use (OTA 1984:165-166; Houseal, MacFarland, Archibold and Chiari 1985:11). Indigenous peoples are encouraged to utilize the outer rings of the reserve and to help protect the permanent core in the center. The best examples in Mesoamerica are the Mapimí and La Michilía Biosphere Reserves in Mexico and the Río Plátano Biosphere Reserve in eastern Honduras (Halffter 1980, 1981a, 1981b; Glick and Betan-

court 1983). Indigenous people who live in the reserve have been included in its planning and operation so that they have a stake in its success. They serve as the primary guards of the buffer zone between the pristine forest in the core and the destructive human activities outside the reserve. Reserves based on this model have also shown promise in Panama and Costa Rica, and the Montes Azules Biosphere Reserve in Chiapas, Mexico will most likely follow this pattern.

The crucial point here is that local people must be included in the development of these conservation units, and those areas must contribute to the welfare of surrounding populations, if we expect them to survive. If people have to farm inside national parks to stay alive, you can bet that they'll do so.

Our challenge, then, is the difficult task of combining conservation with the sound development of surrounding areas. In Panama, the Kuna Indians of the Comarca de San Blas are providing another good example of how this can be done. On their own the Kunas declared their tribal lands—more than 3,100 km^2 of rainforest—a natural forest reserve to be protected as forest forever. The Kunas are now getting technical and financial support from international organizations, but they are the main force behind the program, because they know that this plan will produce jobs and income for the Kuna community, while it simultaneously helps preserve their cultural identity and their rainforest environment (Chapin and Breslin 1984).

These solutions are only first steps. There is still a long way to go. But by supporting the right to exist of the remaining rainforests and rainforest peoples, we can help assure the survival of this vital ecosystem and the cultural survival of the people who live within it. At the same time, we'll be protecting the health of our planet.

Those of you in this room can help achieve these goals by learning about ecological problems like tropical deforestation and by supporting organizations that are dedicated to conservation and sound development. Join organizations like the World Wildlife Fund, the Sierra Club, the National Wildlife Federation, Friends of the Earth, Greenpeace, Audubon, Earth First!, The Conservation Foundation, the Nature Conservancy—whichever group fits your particular bias. Support organizations like Survival International, the Anthropology Resource Center, and Cultural Survival that are dedicated to indigenous human rights.

Finally, find out how your career fits in. Those of you who are scientists, writers, photographers, social scientists, geographers, anthropologists, economists, whatever—you can use your skills and your position to publicize the plight of natural ecosystems like tropical rainforests and the people who live in them. Short of nuclear war, the most crucial problems we'll face during the rest of our lives are ecological problems like food production, population growth, and ecosystem destruction. These problems are incredibly complex, but there are none that are more important. My challenge to you is that it is to our advantage, both as individuals, and as fellow members of the human species, to understand these problems and to work together toward solving them.

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An Economic Perspective on Tropical Deforestation

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I. Introduction

Tropical deforestation is not only a major environmental problem throughout the Third World, it is a critical development problem as well. Tropical forests have declined by nearly half in this century, and in most countries of Africa, Asia, and Latin America, the net rate of forest loss is rising (1). The underlying causes of deforestation are complex, involving economic, social, political, and institutional factors that affect forest resource use. Although these factors vary in importance from one region to another, the result is the same. Potentially renewable forest resources are being treated as nonrenewable resources due to harvesting rates that exceed regeneration and planting rates. Forest resource stocks are being depleted, and the environmental benefits of forests diminished or lost.

Deforestation is a growing threat to Third World development because it affects many areas of economic activity and human welfare. Tropical forests are closely linked to many subsistence and commercial activities through the raw materials they provide and the environmental services they perform. Because of these physical linkages, the forest-depleting activities of individual resource users can have widespread impacts. As deforestation progresses, agricultural productivity declines, energy supplies are disrupted, even human health is impaired. This is adversely affecting the daily lives of nearly two-thirds of the world's population and imposing significant costs on developing country economies.

This paper focusses on the economic dimensions of tropical deforestation, and the need for new analytical approaches to help guide efforts to solve it. Clearly, economics is but one of several important perspectives on the problem. Social, political, and institutional factors, both within and outside the forestry sector, that contribute to deforestation must also be addressed if lasting solutions are to be found (2).

II. Underlying Economic Forces

A fundamental economic problem underlies the activities contributing to deforestation—the private costs of forest exploitation do not reflect the costs incurred by society as forests are depleted. This divergence between private and social returns stems from the inability of markets—due to market failure or distortion of market incentives—to provide proper signals to individuals that would lead to an "optimum" level of forest resource use.

There are three major sources of this divergence. First, forest exploitation can have potentially large and widespread physical impacts, such as increased downstream erosion and sedimentation from loss of upland forests. These impacts, or "externalities," impose costs that individual resource users do not adequately account for. Because society bears the costs of these external impacts, they have no effect on individual behavior. Second, in most developing countries there is open access to common property forest lands. In the absence of property rights under open access, individuals have no incen-

tive to regulate their use of forests or to internalize the costs from externalities. Third, many countries have policies that distort market incentives and actually promote forest depletion. Because of externalities, open access, and inappropriate policy incentives, the economic (social) costs of forest depletion are significantly understated or ignored.

Physical Linkages and Externalities.

There are many physical linkages between tropical forests and human activities. Forests provide resources that are critical to meeting the daily needs of the rural and urban poor, and are an important source of raw materials for small and large-scale industrial uses. By protecting soil and water resources, forests help sustain the capacity of the environment to support agriculture and other sectors. Deforestation disrupts these physical linkages and externalities arise. The problems are familiar, such as fuelwood scarcity and soil erosion. What is less recognized, but of great importance, is the integrative nature of these problems. Impacts in one sector can have effects in another. The following is an overview of the direct and indirect impacts of deforestation (3).

1. *Agricultural impacts.*

Deforestation seriously impacts agricultural production through its effects on soil and water resources, fuelwood supplies, and the availability of tree fodder. These impacts differ in importance from one region to another.

Loss of environmental stability. The loss of forest cover on upland watersheds and semi-arid and humid lowlands reduces environmental stability and leads to degradation of the soil and water base for food production. An estimated 160 million hectares of upland watersheds have been seriously degraded throughout the developing world. The loss of upland forest cover has both on-site and downstream impacts. On-site soil erosion increases, reducing the productivity of the land. Downstream agriculture is threatened by effects on the water regime. Without the protection of forest cover, the regulation of stormflows is reduced or lost. The interception and storage of water by the roots and soil humus layers, and its release as a sustained flow of water to streams, is replaced by increased peak flows and surface water runoff. This, in turn, leads to increased soil erosion and sedimentation of rivers, which can intensify flooding in the lower reaches of rivers and result in widespread damage to lowland agricultural areas. The increased downstream transport of silt and debris from degraded uplands does considerable damage to critical storage reservoirs and irrigation developments, disrupting their operation and reducing their useful lifetime. In addition, disruption of the temporary storage and regulated flow of water leads to reduced dry season river flows available for irrigation. This has significant impacts on areas dependent on irrigated agriculture and is a constraint to the further spread of irrigation.

Large areas of the humid tropics have forest soils that are not capable of supporting continuous cultivation because of low fertility and poor structure. These areas would be properly considered marginal lands. The principal method of agriculture is shifting cultivation, in which forest areas are cleared and the vegetation burned to release nutrients to the soil. These areas are cultivated for two or three years, or until the accessible nutrients in the soil are

used up and crop yields begin to decline, and then are left to recover. As trees regenerate during the fallow period, they play a vital role in restoring nutrient cycles by drawing nutrients to the surface with their deep roots.

Forest loss, population growth, and other pressures have forced farmers to lengthen cropping periods and shorten fallows in shifting cultivation systems, allowing insufficient time for forest recovery. This breach in the natural cycle of regeneration leads to land degradation and a sharp reduction in crop yields.

In semi-arid and arid lowlands, deforestation is having severe impacts on agriculture. Because of the fragility of the soil and low and erratic rainfall, these areas have lower carrying capacities for people and their livestock and are particularly sensitive to human abuse. Wind is the primary agent of erosion. With the loss of tree cover, wind erosion increases and the moderating effects of trees on dust storms and sand dune formation are lost. This leads to a decrease in soil moisture and greater crop damage. The loss of trees also reduces the effectiveness of rainfall by decreasing the amount of water that percolates into the ground. Water runoff increases, erosion accelerates, the water table is lowered, and springs and wells dry up. Together with overgrazing and continuous cropping of marginal land, this exacerbates the effects on food production of periods of low rainfall or drought.

In its most extreme form, deforestation leads to desertification—a process of decline in the biological productivity of semi-arid and arid lands. Desertification is undermining the food-producing capacity of drylands throughout Africa, Asia, and Latin America. An estimated 1.3 billion hectares are at least moderately desertified in these three regions, and more than 300 million people live in areas at least moderately or severely desertified.

Fuelwood scarcity. Increasing scarcity of fuelwood supplies in upland hill areas and semi-arid lowlands significantly affects food production in two ways. First, as fuelwood becomes scarce the only readily available alternative for many families is to burn crop residues and animal dung. In small-holder farming systems, crop residues and dung are normally applied to crop fields to help maintain the productivity of the soil. Their use as fuel robs the soil of badly needed organic matter and nutrients and leads to poor soil structure, lower retention of available nutrients in the crop root zone, and reduced protection from the erosive effect of heavy rainfall. The failure to maintain soil productivity leads inevitably to declining crop yields. A second impact of scarcity is the increasing time that must be devoted to collecting fuelwood. Gathering and transporting fuelwood increasingly dominates the daily lives of millions of people in rural areas, particularly women and children. This shortens the time available for weeding and tending crops.

Loss of tree fodder. Deforestation negatively affects agricultural productivity through the loss of forest fodder supplies. Tree fodder plays an important role in many farming systems. It can be a valuable source of mulch for maintaining the productivity of croplands. In many upland areas forest fodder is also an essential source of feed for draft animals. As supplies dwindle, draft animal power is reduced. In semi-arid regions, tree fodder can account for a significant portion of the livestock feed requirements of migrant populations. Deforestation has resulted in

shortages of animal feed and forced migration away from degraded areas.

2. *Energy impacts.*

Deforestation is affecting the energy supplies of both rural and urban populations, subsistence and commercial users.

Wood energy. An estimated 1.5 billion people, or 70% of the 2 billion people who rely on wood to meet a major part of their household energy needs, are cutting wood faster than it is growing back. Some 125 million people cannot find enough wood to meet their needs, even by overcutting the forests. Thirty-four of the countries with fuelwood shortages have no proven oil or gas reserves, which, combined with low GNP per capita and low rates of economic growth, severely constrains their ability to switch from traditional biomass fuels to fossil fuels.

In urban areas, most households must buy fuelwood or charcoal. Prices have risen sharply in recent years as the circle of deforestation around cities and towns widens and fuelwood and charcoal must be transported over greater distances. In many areas, between 20 and 40 percent of the cash income of the average urban household must be set aside to buy wood or charcoal.

Hydroelectric supply. Hydropower plays a significant role in the electricity generation systems of many developing countries, and is particularly important in helping to reduce demand for imported oil or coal. Dams and generating facilities are major capital investments. In Asia, planned investments in hydropower development over the next decade total nearly $42 billion. As noted above, the loss of forest cover on upland watersheds disrupts the water regime and leads to increased flooding, soil erosion, and sedimentation of rivers. This is damaging reservoirs and accelerating the rate at which they are filling up with silt. The economic lifetime of many dams is being sharply reduced, and the supply of badly needed hydropower is being disrupted.

3. *Industrial forestry impacts.*

Industrial wood products such as sawnwood, plywood, and pulpwood are a source of essential building materials and of the paper needed for schoolbooks, newspapers, packing, and other uses. In addition, forests supply numerous so-called "minor" forest products that have a wide range of industrial applications. These include canes and fibers, essential oils, gums, resins, latexes, waxes, and tannins and dyes. Sustained development of the Third World implies a steady growth in demand for industrial forest products as literacy spreads and the needs for housing, paper, and other goods increases.

The depletion of commercial forest stocks in many developing countries is having serious economic consequences. Current levels of forest management and reforestation fall far short of what is needed to limit imports and sustain exports. Small-scale artisinal activities based on forest resources are affected as well.

Rising imports and declining exports. Deforestation is leading to a growing inability of many countries to meet their domestic needs for industrial forest products. Imports are increasing sharply, even in such countries as Nigeria, Thailand, and Mexico that should be readily able to supply their own needs. Nigeria, once a significant exporter of timber, now imports industrial forest products at a cost of more than $210 million annually. Overall, developing country imports rose from about $6 bil-

lion in the early 1970s to almost $10 billion in 1983.

Deforestation threatens developing country exports of industrial forest products, which are an important source of foreign exchange and rank fifth overall in non-oil exports. In a number of countries, notably Cameroon, Gabon, Ivory Coast, Malaysia, and the Philippines, current rates of timber harvesting and insufficient investment in management and reforestation will lead to a sharp decline in exports within 10-15 years. By the end of the century, the 33 developing countries that are now net exporters of forest products will be reduced to less than 10, and total developing country exports of industrial forest products are predicted to drop from their current level of more than $7 billion to less than $2 billion. This will have a significant impact on employment and income.

Small-scale artisinal activities. The extent of artisinal and other small-scale commercial enterprises based on forest products has received little study. However, it is becoming increasingly apparent that activities such as furniture-making, handicrafts, and charcoal production are a significant source of employment and income. In many countries, this represents one of the most important sources of employment after farming. The costs of deforestation in terms of its impact on these activities are vastly understated.

4. *Health impacts.*

Deforestation is affecting the health of rural and urban populations in developing countries through its impacts on nutrition and domestic water supply. Although impossible to quantify, deforestation affects the health sector in developed countries as well by reducing the stock of genetic resources of potential use in pharmaceutical development.

Nutrition. The effects of fuelwood scarcity and other impacts of deforestation on food production have already been noted. Fuelwood scarcity can have other important effects on nutrition. With the rising cost of fuelwood and charcoal in urban centers, and increasing scarcity in rural areas, many families are forced to alter eating patterns to an extent that impairs their health. Families may eat less nutritious quick-cooking foods. In other cases, the frequency of cooked meals has to be reduced, or food is inadequately cooked which reduces its digestibility and increases the threat of disease. Deforestation also affects food supplies through the loss of foods directly available from the forest. This is particularly significant in areas where forest wildlife accounts for a major portion of animal protein supplies.

Water supply. Deforestation affects the quantity and quality of domestic water supplies. This, in turn, impacts the health of large numbers of people, particularly in urban centers. The disturbance of water regimes from the loss of forest cover disrupts the steady supply of clean water, leading to shortages in the face of rising demand and the threat of disease. Water-borne diseases remain a major cause of infant mortality in the Third World.

5. *Biological impoverishment.*

Tropical moist forests harbor an estimated 50% of the world's plant and animal species. This wealth of biological diversity is a vast storehouse of genetic resources. Although less than one percent have been screened for their potential usefulness, tropical forest species have already made enormous contributions to agriculture, medicine, and in-

dustry. For example, wild genetic relatives of many modern food crops are found in the tropics. These wild relatives, and genes from other forest plants, can be used to genetically improve food crops as a means to increase productivity, to increase resistance to pests and diseases, or to increase their ability to withstand environmental stresses. In addition, tropical moist forests remain the world's primary source of raw materials for pharmaceutical development. Almost one out of five pharmaceutical products derives in one way or another from tropical moist forest plants and animals. Among the thousands of drugs fo tropical origin are some of the most significant cancer treatments yet developed.

Tropical species and populations are highly vulnerable to extinction through habitat destruction and other disturbances because of their limited and often patchy distribution. In addition to the outright extinction of species (or local populations of species), the fragmentation of tropical moist forest habitat into isolated patches can accelerate species loss (and the loss of genetic diversity) by disrupting the structure and dynamics of these complex ecosystems, setting in motion a gradual process of biological impoverishment.

Although difficult to quantify, the loss of biological diversity through deforestation has significant economic implications. Logic dictates that the 99 percent of tropical forest species that have yet to be studied will yield far greater benefits than the 1 percent that have already been utilized. Several wild and domesticated food plant varieties have become extinct and many more are seriously threatened. The continued loss of biological diversity will limit opportunities to broaden the genetic base for agriculture, medicine, and industry.

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Historically, forest lands in developing countries have been primarily a common-property resource. Resource management systems evolved that effectively regulated access to and exploitation of common-property forests, thereby preventing their depletion. For example, traditional methods of shifting cultivation within tropical forests, involving long fallow periods to allow forest recovery after cultivation and to restore productivity, are known to have been ecologically sound and sustainable systems. These traditional systems of common-property resource management have broken down under the combined pressures of internal and external social, economic, and political forces (4).

Rapid population growth has been an important factor in the breakdown of traditional resource management systems. Of equal importance in many areas, however, have been the effects of external political and commercial domination. The social organization of many traditional societies was weakened or destroyed during the colonial era. In addition, resources that were exploited primarily to meet subsistence needs became "monetized," leading to much more intensive rates of exploitation.

The destructive effects of colonialism have been exacerbated by national governments in many countries. Throughout the Third World, the ownership, control, and management of forests has shifted from local communities to national governments. Close to 80% of forest lands in developing countries are now state owned and under management of government agencies, primarily forestry departments (5). However, in most developing countries, these agencies are typically of recent origin and are relatively weak.

Planning and regulation of forest conservation and development programs is generally inadequate or ineffective.

With the breakdown of traditional resource management systems and the constraints to effective forest regulation by government agencies, forests are being exploited under open-access or virtually open-access conditions over much of their extent. Under open-access conditions, there is an absence of some form of property rights associated with resource use. This undermines individual incentives to reduce or regulate personal consumption of forest resources toward an optimal level of exploitation and to invest in their long term productivity, because the benefits of such action would only accrue to other resource users. Stated differently, each individual has an incentive to ignore the social costs of his resource use for fear that others will capture the benefits of the resource before he can. The absence of some form of regulated access to forests, combined with increasing resource demand associated with population growth and unequal access to agricultural land and other resources, results in a rate of aggregate use that exceeds the rate of forest renewal.

Inappropriate Policy Incentives

Government policies in many developing countries toward forest exploitation, and toward land use activities that lead to conversion of forests, have created virtual open-access situations and are a driving force behind deforestation. Governments are directly or indirectly subsidizing deforestation through economic policies—such as investment incentives, tax and revenue systems, credit programs, and government pricing—that lower the net costs or increase the private profitability of forestry and competing land use activities. These powerful economic incentives induce individual resource users to unduly favor short-term consumption over long-term management, leading to much higher rates of forest exploitation and conversion than would be the case without such policies (6).

Forest revenue systems, including the terms of forest concession agreements through which private timber operations gain access to public forests, can encourage rapid and wasteful exploitation in several ways. Commercial species in a virgin forest often have a high value because they are freely provided by nature. Whatever market value they have above the costs of harvesting, transport, and processing, is profit. In many countries with considerable forest resources, government forest revenue systems (royalties, taxes, fees) fail to adequately capture these profits, creating strong profit incentives that induce private investors to exploit all the profitable areas they can.

The nature of the charges levied on forest exploitation can also accelerate deforestation. Forest charges are often based on the volume of timber removed from a stand, rather than the volume of merchantable timber available, and do not differentiate between low and high-valued species. This provides an incentive to selectively remove only the high-valued species from a forest stand. This practice of "high-grading" not only depletes forests of high-valued species, but results in significant damage to the remaining trees in the stand since there is no incentive to minimize logging damage.

Another problem is the short time frame of many forest concession agreements, often less than the time required for a single forest rotation. This undermines incentives to sustainably manage

the forest since the contractor does not have a stake in its long-term productivity. This often results in careless logging practices, faster harvest schedules, and lack of investment in reforestation or other management activities. The fact that government forestry departments do not have the means to adequately monitor forestry operations and enforce the terms of concession agreements in remote forest areas only adds to these problems.

Similar forces are at work outside the forestry sector. Many governments have instituted policies that accelerate the conversion of forest lands to other land uses. For example, some countries have "you clear it, you own it" policies whereby farmers can gain property rights to forest land only by clearing it. This promotes expansion of shifting cultivation by small farmers. These farmers often gain ready access to forests by following on the heals of logging operations that have opened up forest areas.

Countries such as Brazil and Indonesia have undertaken very large-scale commercial agriculture and land settlement programs in forest areas that are supported by massive public subsidies. Multilateral and bilateral development assistance agencies have been major sources of funding for these programs. In the Indonesia transmigration program, the cost of resettling families to sparsely populated forest areas has risen to $10,000 per household. These subsidies increase the relative profitability of other land uses, providing strong economic incentives that accelerate the pace of deforestation. Brazil provides a dramatic example. Enormous public subsidies have led to rapid conversion of forest lands to pasture for large-scale cattle ranching operations. Conversion of forest to pasture accounted for 72 percent of the deforestation detected by Landsat monitoring up to 1980. Many of these cattle ranches have proven to be uneconomic (in addition to environmentally destructive) and after several yeras of operation usually fail, but forest conversion continues because most of the costs are assumed by the government through subsidies.

The divergence between private and social returns due to inappropriate policies toward forest exploitation and competing land uses can be very large. Private resource users reap excessive profits, often at great expense to society. The economic incentives that these policies create lead to lost public revenues, wastage of resources, and excessive public subsidies that do not yield significant public benefits. But the costs to society are even greater. The accelerated pace of forest depletion due to these policies results in externalities that impose significant additional costs.

III. The Need for Public Intervention

Externalities, open-access common property problems, and inappropriate policies lead to a divergence between private and social returns from forest exploitation. This provides strong incentives to over-exploit forests, resulting in depletion of the forest resource stock. The inability of the market to resolve this divergence means that some form of public intervention is needed to provide incentives to change the forest-depleting behavior of small and large-scale resource users. This is not meant to imply that only public sector solutions are feasible or desirable. It does mean that government leadership is essential to creating a policy and investment environment that will promote sustainable patterns of forest land use by both pub-

lic and private resource users. Similar efforts by the development assistance community are needed, which has a critical role to play in helping governments tackle these problems.

Although there is a growing awareness of the urgency of tropical deforestation, the response of most developing country governments and the international community falls far short of what is needed to address the problem. Forestry and agroforestry remain a relatively low investment priority. Most countries have forestry budgets that amount to less than two percent of their respective annual expenditures within the agriculture and energy sectors. The situation is largely the same within the development assistance agencies.

Why have governments and the development assistance community failed to respond? The reasons are many and varied, encompassing political, economic, social, and institutional factors. However, the inadequate response to date is due in no small part to a lack of political awareness of the role of forests in development and the economic and social consequences of forest depletion. Decision makers are rarely presented with an integrated overview of forestry issues and the consequences of forest mismanagement.

Efforts to address deforestation have focused largely on remedial measures through investment projects. These efforts must be greatly expanded. However, the project approach alone is inadequate because it does not address the fundamental causes of deforestation. Policies and incentive structures that influence forest land use and underlie forest depletion must simultaneously be addressed.

This requires changes in the conceptual framework and analytical approaches of development planning. The lingering view that issues of environmental protection are somehow "external" to the development process must be changed. Sustainable management of forest resources must be considered essential to achieving long-term development objectives, and should become an integral component of economic and social policy and macroeconomic planning. This requires a clear understanding of the economic costs of deforestation and the economic benefits of sustainable forest management. An expanded approach to economic analysis is needed that accounts for the true costs and benefits of forests and their use, and that can help guide efforts to initiate new policies and investment programs to address the underlying causes of deforestation.

An Expanded Approach to Economic Analysis

Economic analysis plays a central role in decisions that in large measure determine, and will continue to determin, the fate of tropical forests. All countries face the basic problem of how to allocate scarce resources to a variety of different uses in order to maximize the net benefit to society. Economic analysis can provide a convenient and consistent method for evaluating alternatives by assessing their costs and benefits and reducing them to a common measure for comparison.

However, the prevailing framework for economic analysis does not provide a sound basis for decisions related to forest resource use, and in fact is an important factor in their widespread misuse. Economic analysis as currently practiced fails to account for forest goods and services that do not have a market price, and generally ignores extra-market effects both now and in

the future. As a result, alternatives to mitigate these costs and the benefits of protecting and sustainably managing forests are undervalued.

The objective of an expanded approach to economic analysis is to provide decision-makers with as complete a picture as possible of the social costs and benefits of forests and their use. The analysis should provide information relevant to the needs of decision-makers and in a useable form. This requires practical methodologies for deriving operationally useful measures of the value of non-market goods and services.

Marginal opportunity cost as an analytic tool. A practical way to evaluate in economic terms the social costs of deforestation is to apply the concept of "marginal opportunity cost." The marginal opportunity cost of resource use is the cost to society of a marginal reduction in the stock of a given resource. Economic theory tells us that this cost should be equal to the price that individuals have to pay to utilize the resource. A price less than the marginal opportunity cost will stimulate overexploitation.

The marginal opportunity cost of resource use has three components—the marginal *direct* cost, the marginal *user* cost, and the marginal *external* cost. The direct cost is the cost to the user of harvesting the resource and is measured by the value of foregone output or leisure. The user cost component is the cost to future users of depleting the resource stock today. This can be evaluated in terms of the marginal cost of reestablishing the resource (for example, the marginal cost of reforestation) or of replacing the resource (for example, substituting kerosene for fuelwood). External costs are the costs imposed on others due to externality effects of resource use (as described in Section II above).

In deriving operationally useful measures of the "true" cost of forest resource use, the marginal external cost component is particularly significant. To estimate the marginal external cost of forest depletion, it is necessary to attach market values to non-market goods and services. This requires breaking down these goods and services into their physical characteristics, and relating changes of these characteristics (due to the physical effects of deforestation) to the production process of relevant commodities that are actually traded and have a value expressed as a market price.

To illustrate, consider the external effect of deforestation and reduced fuelwood supply on agricultural productivity. As described earlier, households respond to fuelwood scarcity by burning animal dung and crop residues that normally are used to help maintain soil productivity. The result is a decline in crop yields.

To calculate the marginal external cost from dung being used as a fuel instead of as a fertilizer would entail the following general steps:

(1) Determine fuel equivalent values for dung and wood;
(2) Determine fertilizer equivalent values for dung;
(3) Determine the incremental crop yield response for a unit input of dung (based on fertilizer response curves);
(4) Calculate lost agricultural output due to the marginal impact of fuelwood depletion on reduced fertilizer (dung) application.

The market value of this foregone output represents part of the marginal opportunity cost of deforestation.

Limits to Economic Analysis

To most effectively use economic analysis as an aid to decision-making, it is important to recognize its limitations. There are circumstances in which even an expanded approach to economic analysis can produce incomplete or misleading results.

Lack of biophysical data. To calculate the marginal opportunityu cost of forest depletion requires a thorough understanding of the complex physical linkages associated with deforestation. The need to integrate physical and biological considerations with economic analysis can present significant measurement problems. The biophysical data required for these calculations is often inadequate, particularly in developing countries that have not had the means for systematic collection of such data. Related to this is the paucity of knowledge of the workings of tropical ecosystems. Another complicating factor is the often location-specific nature of the impacts of deforestation, making generalizations difficult and the need for local data even greater.

As important as these constraints can be, they should not prevent attempts to account more fully for the social costs of deforestation. It is not necessary to quantify all physical relationships in the analysis. Often, the appraisal of just one or two extra-market effects is sufficient to give a significantly more accurate picture of benefits and costs. In addition, exact quantification is not required, nor are very technically sophisticated approaches. Of greater importance is the analytical process of taking into account as many relevant costs and benefits as possible. The use of sensitivity analysis to test assumptions can help overcome the uncertainty associated with limited data.

Irreversible effects and inter-generational equity issues. An important limitation to economic analysis is the treatment of inter-generational equity issues. Appraising the welfare effects of forest depletion on future generations poses major conceptual problems. Future benefits and costs must be expressed in present value terms. This requires the use of a discount rate, which is based on the opportunity cost of capital. Because the opportunity cost of capital is high, especially in developing countries, discount rates of 10 to 12 percent are commonly used in benefit-cost analyses. Discounting at this rate discourages investments with long-term benefits, while promoting projects with long-term costs. As a result, short-term economic interests are often favored at the expense of longer-term environmental concerns. Coping with inter-generational equity issues is most difficult where irreversible effects are involved. There is no clear understanding of how to appraise the costs of irreversible effects of deforestation, such as species extinction, or of how to evaluate the preferences of future generations. In such cases the marginal opportunity cost approach must be supplemented by other analytical methods and perspectives.

As a general rule, the greater the uncertainty about future preferences, the greater the weight that should be given to preserving future options. Although of limited use in clarifying future preferences, expanded economic analysis nevertheless can play an important role here. A more comprehensive accounting of the short-run benefits and costs of forests and their use should result in policies and investment decisions that to a greater extent will preserve options for future generations.

IV. Conclusion

Powerful economic factors are a driving force behind tropical deforestation. To address these factors requires changes in the prevailing approach to investment and policy decisions, which is based largely on conventional benefit-cost analysis. An expanded approach to economic analysis, based on the concept of marginal opportunity cost, will provide a more complete picture of the economic costs of tropical deforestation and the economic benefits of sustainable forest management. Although this approach involves conceptual and estimating problems, much more can be done using known techniques than is now being attempted.

The marginal opportunity cost of forest depletion has several important policy and investment implications. First, marginal opportunity cost can serve as an economic indicator of forest resource scarcity. That is, the higher the marginal opportunity cost of resource use, the more scarce a resource is relative to the demand for it. This can provide policy guidance to decision-makers and indicate priority areas for investment. Second, marginal opportunity cost can reveal the extent to which market prices do or do not reflect the social cost of forest resource use, and hence the extent to which markets approach or diverge from an optimal allocation of resources in terms of long-term sustainable use. Finally, the most far-reaching implications of an expanded approach to economic analysis will be in the realm of multi-sectoral policy and planning. Evaluating the physical linkages between forest resource use and agriculture, energy, and other sectors will demonstrate the need for more integrative, multi-sectoral approaches to policy-making and investment project planning. Only through a sustained commitment to forestry, agriculture, energy, and related rural development efforts can current trends in tropical deforestation be reversed.

Notes

1. In this paper, "tropical forests" refers to forests and trees in the humid and semi-arid/arid areas of developing countries. Thus, the term includes forest formations ranging from moist (or closed) tropical forests to dry (or open) woodlands.
2. There are important dimensions to the problem of tropical deforestation beyond purely utilitarian concerns, such as aesthetic and ethical issues associated with the destruction of natural habitats.
3. The review of the direct and indirect impacts of deforestation is based largely on "Tropical Forests: A Call for Action, Part 1," World Resources Institute, Washington, D.C., 1985.
4. R. Repetto and T. Holmes, "The Role of Population Growth in Resource Depletion," Population and Development Review, IX, December 1983, 609-632.
5. J. P. Lanly, "Tropical Forest Resources," FAO Forestry Paper No. 30, U.N. Food and Agriculture Organization, Rome, 1982.
6. This section is based on R. Repetto, "Creating Incentives for Sustainable Forest Development," World Resources Institute, Washington, D.C., (forthcoming).

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THE AQUATIC DRYOPOIDEA OF LOUISIANA (COLEOPTERA: PSEPHENIDAE, DRYOPIDAE, ELMIDAE)

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The Aquatic Dryopoidea of Louisiana (Coleoptera: Psephenidae, Dryopidae, Elmidae)[1]

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Abstract

A study of the aquatic Dryopoidea of Louisiana was conducted to determine species composition and distributional factors. From May 1979 to May 1981, 195 collections were taken at 191 sites in 59 of the state's 64 parishes with emphasis on lotic waters. Aquatic dryopoids were collected at 138 of these sites in 39 parishes. Additional records, collected either before or after the study through June 1984, are also reported. Twenty-five species were found to occur in the state: 1 Psephenidae, 4 Dryopidae, and 20 Elmidae. Twenty-two are reported for the first time, including one undescribed species of *Stenelmis* and 3 species of *Dubiraphia* that are possibly undescribed. Most of these are eastern and coastal plain species; none is western. Brief descriptions and a key to the species are provided, and several taxonomic problems are discussed. The 5 most common species in the state were *Stenelmis grossa* Sanderson (63% of collections), *Macronychus glabratus* Say (44%), *Ancyronyx variegata* (Germar) (35%), *Stenelmis bicarinata* LeConte (31%), and *Microcylloepus pusillus* (LeConte) (25%).

Species distribution within the state was examined in relation to vegetation patterns, physiography, and drainage basins. Twenty-four species occurred in pinelands, 16 in the alluvial plain, 13 in upland hardwood areas, 9 in oak-pine areas, 5 in the prairie, and one in the deltaic plain. The Lake Ponchartrain and Pearl River drainage basins had the greatest number of species, 20 and 21, respectively. Macro- and microhabitat preferences are reported for each species. The largest number of species were collected from streams with mixed sand and gravel substrates. Adult and/or larval dryopoids were found every month of the year except January. It is probable that both stages of all species occur year-round in Louisiana streams.

Introduction

The aquatic dryopoid beetles function as important members of the lotic community in streams and rivers and are represented in Louisiana by the families Psephenidae, Dryopidae, and Elmidae. Aquatic members of the superfamily Dryopoidea typically inhabit riffles or rapids; however, several species prefer pools, a few may occur in lakes, and one species (*Pelonomus obscurus* LeConte) is strictly lentic. The common name riffle beetles is often applied to the group as a whole (Brown, 1976, 1987a).

Previous records and preliminary collecting indicated that the aquatic Dryopoidea are widely distributed in the state, exhibiting abundance and diversity of species in suitable habitats. This paper, based on the thesis project of the senior author (Barr, 1981), represents the first comprehensive study of the aquatic dryopoid fauna of Louisiana. Records of specimens collected outside of the study are also reported. Different geographical features of the state such as vegetation patterns, physiography, and drainage basins were examined in an effort to explain observed distribution patterns. Collections were made year-round so that seasonal and monthly occurrence could be documented. Many taxonomic problems exist within this group, several of which pertain to Louisiana species.

Life History

The life histories of most species are poorly known although several recent papers have been published (LeSage and Harper, 1976a, 1976b, 1977). A general overview of the biology of the Dryopoidea has been given by Brown (1976, 1987a). Most adult and larval

[1]Approved for publication by the Director of the Louisiana Agricultural Experiment Station as manuscript number 86-17-0320.

elmids, adult dryopids, and larval psephenids are aquatic; larval dryopids and adult psephenids are semi-aquatic or terrestrial. Aquatic elmid larvae have at least 5 larval instars. Pupation is terrestrial in all 3 families and occurs under logs, debris, and stones along the shore. Emerging adults of many species are attracted to lights. Adults of some species are flightless because the hind wings are vestigial or absent; other species include both alate and flightless forms. After entering the water, most adult elmids (Elminae) remain permanently waterbound, while some dryopids emerge periodically to fly at night. The typical elmid life cycle in Canada may last 3-4 years with one year spent in the adult stage (LeSage and Harper, 1976a). Laboratory survival of adult and larval elmids for more than 3 years has been recorded (Brown, 1973).

The aquatic stages are substrate clingers and are unable to swim. Long claws and streamlined or flattened bodies enable the beetles to grasp objects and move about even in strong currents. The various species inhabit a range of substrates, or microhabitats, such as waterlogged wood, leaf litter, root masses, aquatic plants, gravel, and rocks (Brown, 1966). Doyen and Ulrich (1978) classify the dryopoids trophically as "collector-gatherers" and "scrapers," feeding on either decomposing organic matter or periphyton, which includes algae and diatoms.

Respiration in adult elmids and dryopids employs a hydrofuge ventral plastron functioning as an external gill into which oxygen diffuses directly from the water. This air store is in direct contact with the spiracles. Respiration in adult dryopoids was examined by Harpster (1941, 1944), Davis (1942), Thorpe and Crisp (1949), and Thorpe (1950). The larvae of elmids and eubriine psephenids possess caudal tracheal gills which are retractile into a chamber closed by an operculum. Psephenine and eubrianacine psephenid larvae have external, ventral abdominal gills.

Various aspects of dryopoid ecology have been investigated by Sinclair (1964), Brusven (1970), Murvosh (1970), Davis and Finni (1974), Cowell and Carew (1976), Reisen (1977), Seagle and Hendricks (1978, 1979) and Seagle (1980).

Water Quality Requirements

The water quality requirements of aquatic dryopoids have been discussed by several authors. In general, the presence of the group has been considered indicative of clean water conditions (Gaufin and Tarzwell, 1952, 1956). Young (1961) stated that elmids are ". . . extremely sensitive to even mild pollution and quickly disappear from streams which receive even moderate amounts of industrial wastes." Hilsenhoff (1977) reported 17 species in Wisconsin, all from streams with excellent (clean, undisturbed) to fair (moderate enrichment or disturbance) water quality. The reaction of several dryopoid species to factors influencing water quality has led to their inclusion in lists of water quality indicator organisms. Ten taxa of dryopoids were listed by the United States Environmental Protection Agency in a macroinvertebrate pollution tolerance chart with ratings of intolerant, facultative, or tolerant (Weber, 1973). Mason et al. (1971), in studies of the Ohio River Basin, listed as facultative a genus and a species of Elmidae. Sinclair (1964) reported that several species of elmids are "tolerant of a wide variety of effluents, and may be found even in poorly aerated sections of polluted streams" in Tennessee. Forty species of dryopoids

were included in the EPA's Bio-Storet Master Species List (Weber, 1976), a computer-file directory of water quality indicator organisms.

Aquatic Dryopoids in the Southeastern States and Texas

Information concerning the distribution and biology of aquatic dryopoids in the southeastern states and Texas is fragmentary. Statewide surveys have been conducted in North Carolina, South Carolina, Florida, and Alabama. Twenty-eight species of Elmidae, 5 of Dryopidae, and 3 of Psephenidae were collected in North and South Carolina during a two-state survey (Brigham, 1982). A new species of *Stenelmis* (Elmidae) was described from North Carolina (White and Brown, 1976) and another from South Carolina (White, 1982). Morse et al. (1980) reported 17 species from Upper Three Runs Creek, a tributary of the Savannah River in South Carolina. Water quality information was published for 14 species collected from the Savannah River on the Georgia-South Carolina border by Patrick et al. (1966). Young (1954) listed, described, and provided keys to the 11 elmids and 3 dryopids occurring in Florida. Loding (1945), in a list of Alabama beetles, recorded 6 elmid, 4 dryopid, and 2 psephenid species. The Elmidae of Alabama were more recently studied by Eiland (1979) who furnished descriptions, keys, and natural history observations for 31 species in 9 genera. Brown (1980) described *Alabameubria starki*, a new genus and species of eubriine water penny, from larvae collected in Alabama. In 1979 Lago and Stanford reported *Psephenus herricki* (DeKay) (Psephenidae) as a new Mississippi state record. Eleven genera and 16 species, with notes on habitat and distribution, were reported by Burke (1963) in a preliminary survey of Texas elmids. Brief descriptions, generic picture keys, distributions, and water quality requirements were given by Sinclair (1964) for the elmids of Tennessee. Seventeen species were listed.

Aquatic Dryopoids in Louisiana

Previously, only 2 families (Elmidae and Dryopidae), 7 genera, and 3 species were reported in the literature from Louisiana. Sanderson's (1938) revision of the genus *Stenelmis* included a description of *S. grossa* with paratypes from Louisiana. Hilsenhoff (1973) added 5 new species to the genus *Dubiraphia,* including *D. brevipennis* from Louisiana. In a paper illustrating the North American distributions of dryopoid genera, Brown (1975a) listed 6 genera for the state: *Ancyronyx, Dubiraphia, Macronychus, Microcylloepus, Stenelmis* (Elmidae), and *Helichus* (Dryopidae).

Summers (1874) reported *Pelonomus obscurus* LeConte (Dryopidae) from collections taken in the Lake Pontchartrain region. A species of *Dubiraphia* was found in Ekman dredge samples from Avoyelles Parish during a limnological survey of the Atchafalaya Basin by Bryan et al. (1976). Elmidae were reported from benthic samples and/or fish stomachs by Geagen and Allen (1960) while surveying fish productivity factors in lakes in Caddo, East Carroll, Natchitoches, and Evangeline parishes. Golden (1972), Twilley (1972), Staats (1973), and Rodgers (1977) reported the elmid genera *Ancyronyx. Dubiraphia,* and *Stenelmis* from Jackson and Winn parishes during studies of the effects of paper mill effluent on the fauna of the Dugdemona River. A summary of the published and unpublished literature records, excluding those of Barr (1981), is found in Table 1. Subsequent to this

TABLE 1. Published and unpublished literature records of aquatic Dryopoidea from Louisiana.

AUTHOR	LOCALITY
	FAMILY DRYOPIDAE
	Genus *Helichus*
Brown, 1975a	no localities given
	Pelonomus obscurus
Summers, 1874	Lake Pontchartrain region
	FAMILY ELMIDAE
Geagan and Allen, 1960	Caddo Lake, Caddo P.; Cane River L., Natchitoches P.; Chicot Lake, Evangeline P.; Lake Providence, E. Carroll P.
	Genus *Ancyronyx*
Brown, 1975a	no localities given
Golden, 1972; Twilley, 1972; Staats, 1973; Rodgers, 1977	Dugdemona River, Jackson and Winn P.
	Genus *Dubiraphia*
Brown, 1975a	no localities given
Bryan et al, 1976	Yellow Bayou, Avoyelles P.
Golden, 1972; Twilley, 1972; Staats, 1973; Rodgers, 1977	Dugdemona River, Jackson and Winn P.
	Dubiraphia brevipennis
Hilsenhoff, 1973	Hammond, Tangipahoa P.
	Genus *Macronychus*
Brown, 1975a	no localities given
	Genus *Microcylloepus*
Brown, 1975a	no localities given
	Genus *Stenelmis*
Brown, 1975a	no localities given
Golden, 1972; Twilley, 1972; Staats, 1973; Rodgers, 1977	Dugdemona River, Jackson and Winn P.
	Stenelmis grossa
Sanderson, 1938	Tallulah, Madison P.; Beauregard P.

study, a new species of *Dubiraphia, D. harleyi,* was described by Barr (1984).

Biogeography and Physiography of Louisiana

Louisiana is located entirely within the Gulf Coastal Plain Physiographic Province, with the Mississippi River dividing the state into 2 sections—the East and West Gulf coastal plains (Thornbury, 1965). The area east of the river and north of Lake Pontchartrain is commonly termed the "Florida parishes" (East Baton Rouge, East & West Feliciana, Livingston, St. Helena, St. Tammany, Tangipahoa, and Washington parishes). The Mississippi Embayment (river and associated alluvial plain) has been postulated as a barrier to the westward expansion of several invertebrate and vertebrate species (Bick, 1957; Louton, 1975; Viosca, 1926). Louisiana has the lowest mean elevation of any state in the nation, 100 feet (30 m), with uplands rising to slightly more than 500 feet (150 m). The climate is warm-temperate to subtropical.

Although Louisiana is located in only one physiographic province, much diversity exists in lotic habitats. Clear sandy streams are common in the rolling hills of the north-central, central, west-central, and southeastern parts of the state. Swift, gravelly streams are also present in the "Florida parishes." Although rock outcroppings are rare in Louisiana, soft sandstone and siltstone substrates occur in a few streams in Catahoula, Natchitoches, and West Feliciana parishes. Clay-bottomed channels predominate in the southwestern prairie regions. Muddy, sluggish waters, although common statewide, are the rule in the alluvial and deltaic areas.

Bick (1957) divided the state into 4 physiographic-vegetation zones in a study of the odonate fauna of Louisiana: 1) pinelands, 2) prairie, 3) al-

luvial plain, and 4) deltaic plain. The pinelands in the northwest include the Tertiary Uplands and have the highest elevations in the state. The southeast and west-central pinelands include all but one of the Pleistocene terraces in the state. Most of Louisiana's swift, clear streams are found only in pineland areas. Bick's prairie region in the southwest corresponds to Holland's Prairie terrace. Here the land is flat and mainly used for agriculture; a calcareous hardpan exists near the surface and streams are sluggish and very similar. The alluvial plain extends 25-50 miles (40-80 km) on either side of the Mississippi River north of Lake Pontchartrain, and to a lesser extent along the Red and Ouachita rivers. This plain contains some of the best agricultural land in the state. Forested areas consist of bottomland hardwood tracts including oak, gum, cypress, elm, and hackberry; streams are generally silty and very sluggish. The deltaic plain extends east and west across Louisiana in a band south of Lake Pontchartrain to the Gulf of Mexico. The area is primarily coastal marsh, progressing from fresh to brackish to saltwater. Freshwater habitats are abundant but essentially alike. Most streams, termed "bayous," are muddy and sluggish, and the majority are now channelized. These 4 zones of Bick and

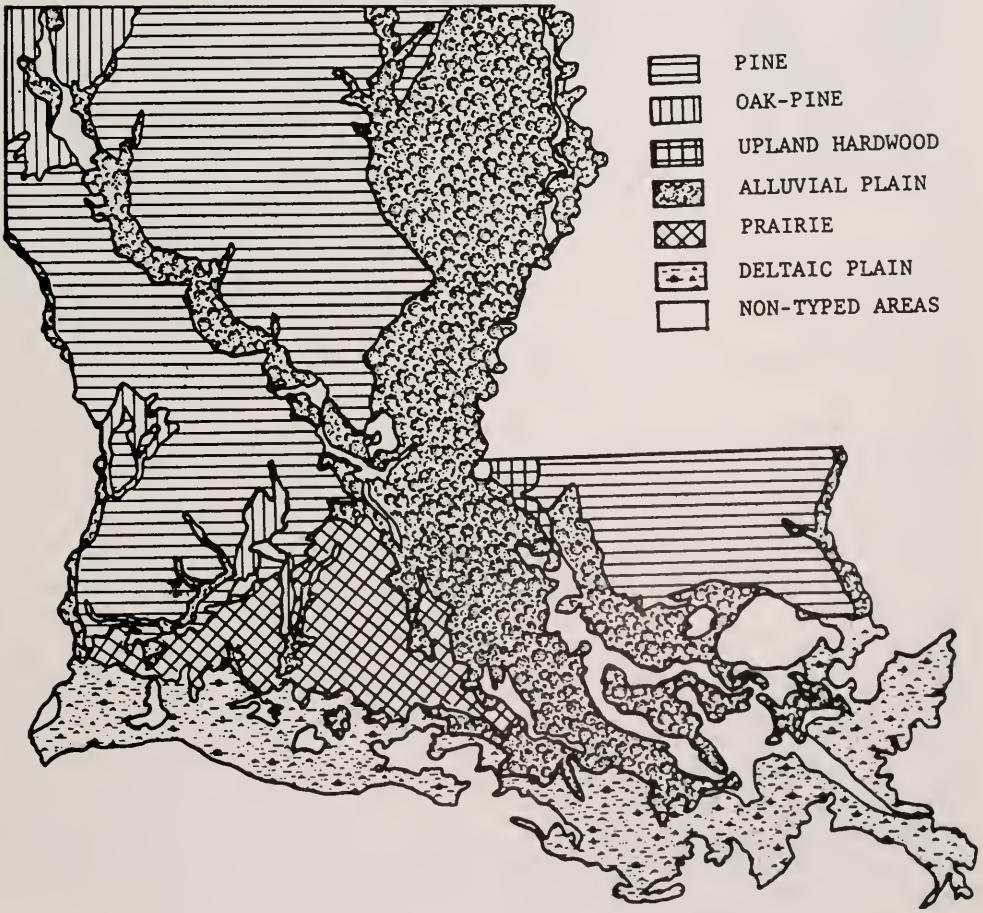


Fig. 1. The major physiographic-vegetation zones of Louisiana.

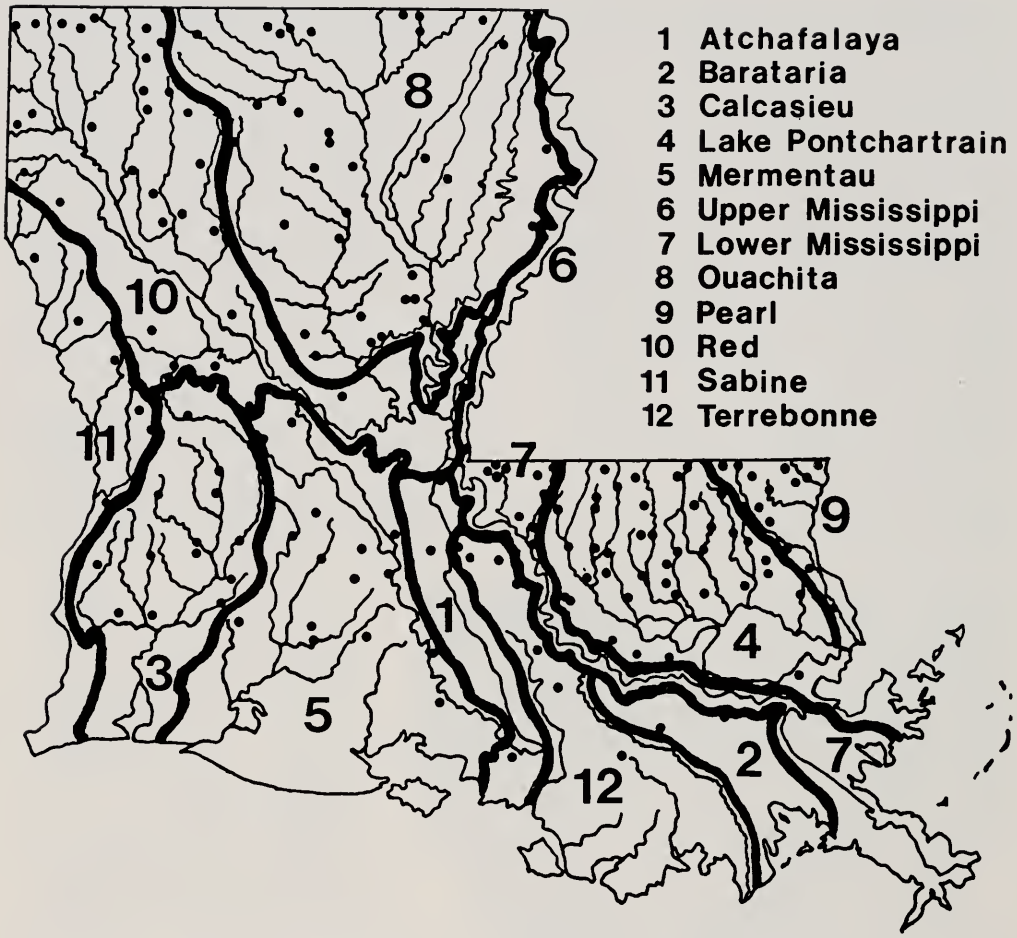


Fig. 2. The distribution of collection sites in the major river system drainage basins of Louisiana.

those appearing on a more detailed map of forest types (Louisiana Department of Natural Resources, 1974) were used in developing Figure 1. In this composite additional upland hardwood, oak-pine, and non-typed areas are distinguished.

The state is divided into 12 watersheds or drainage basins by the Louisiana Department of Natural Resources (1980) (Fig. 2): 1) Atchafalaya River, 2) Barataria Bay, 3) Calcasieu River, 4) Lake Pontchartrain, 5) Mermentau-Vermilion-Teche Rivers, 6) Upper Mississippi River, above Old River, 7) Lower Mississippi River, below Old River, 8) Ouachita River, 9) Pearl River, 10) Red River, 11) Sabine River, and 12) Terrebonne. The Mermentau-Vermilion-Teche Basin is a composite of the drainages of the 3 rivers, and likewise, the Lake Pontchartrain Basin contains the separate watersheds of the Amite, Tickfaw, Tangipahoa, and Tchefuncte rivers. The "Florida parishes" include the latter basin as well as the Pearl River Basin and the upper part of the Lower Mississippi River Basin. The size and percentage of total land area of each basin are included in Table 2.

Materials and Methods

Selection of Sites

One hundred ninety-five collections from 191 different sites in 59 of Louisiana's 64 parishes were made from May 1979 to May 1981 (Fig. 3). Two localities were sampled twice, and one was sampled 3 times. The 5 parishes not sampled are located in the coastal deltaic plain, an area that was found to be generally unproductive for dryopoids. All collections were made by the senior author. Topographic and parish highway maps (Louisiana Department of Transportation) were used to locate and name specific sites. Locality data provided by other aquatic collectors (Bick, 1957; Brown, pers. com., Mar. 6 1979; Louton, 1975; Stewart et al., 1976) were often utilized to pinpoint interesting or unique sites. Detailed locality data are contained in Appendix I. In the Appendices and Systematic Treatment, numbers following the stream or locality name—i.e., (1), (2), etc.—differentiate multiple collections. Since the optimum habitat for almost all species is flowing water (Brown, 1976), collecting efforts were concentrated in streams and small rivers. Large, deep rivers were generally omitted from this survey because of sampling difficulties. Collecting was continual throughout the year.

Stream Types.—Sites were selected to provide a representative sample of the lotic situations and habitat diversity present in Louisiana. A classification of stream types was devised to categorize sites, thereby aiding in the selection process and the examination of data. Pennak (1971), in a synopsis of lotic habitat classification, stated that "perhaps no

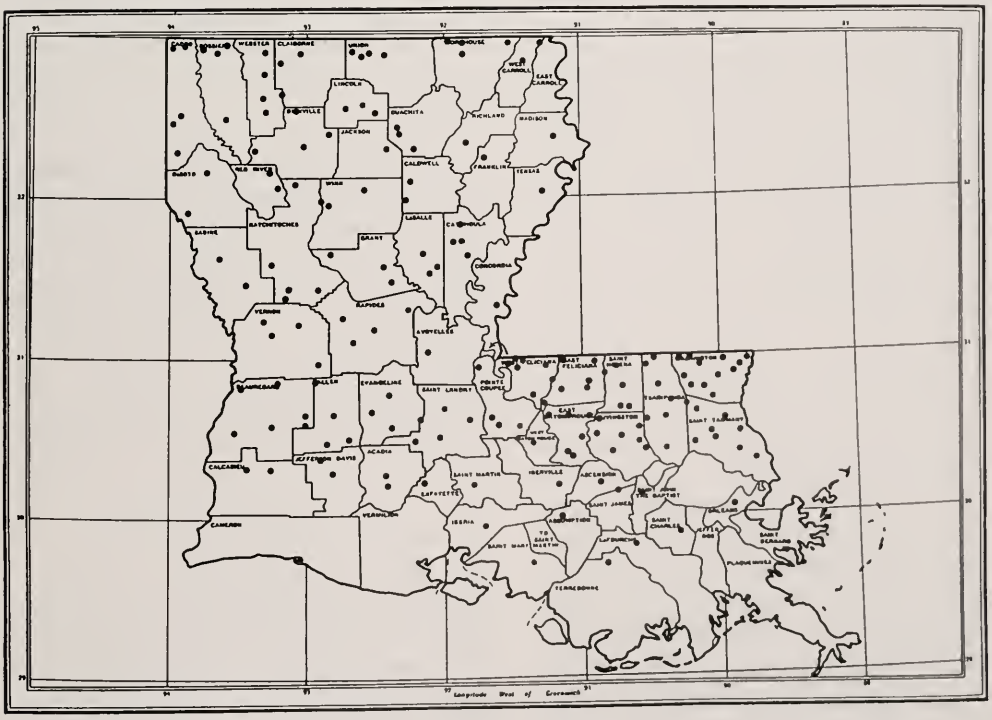


Fig. 3. The distribution of collection sites in Louisiana within parish boundaries.

single factor has greater biological significance than the physical nature of the substrate."

In the course of this study 14 types of streams were defined based on major substrate component (sand, mud, clay, gravel, rock) and size. In reality, streams rarely had uniform substrate compositions, but rather were combinations of 2 or more materials. Mixed sand and gravel streams were more common than either type alone, and it was often difficult to decide which was the dominant component. Streams that were primarily sandy or clayey often had shallow, gravelly riffles or runs, and nearly all had muddy or silty areas. Size designations were based on mean width at the collecting site, i.e., small, 0-20 ft (0-6 m); medium, 20-50 ft (6-15 m); and large, 50+ ft (15+ m). The number of streams of each type and percentage of the total number sampled during the study are given in Table 2. Small sandy streams accounted for 31% and all sandy streams for 48% of the streams sampled. Twenty-six percent were mud-bottomed, 14% were clay, 12% were gravel, and less than one percent were rock. Small, medium, and large streams and rivers accounted for 58%, 31%, and 11% of the total, respectively. The under-representation of rivers was due to sampling difficulties involving water depth.

The depth of a waterbody was often found to be related to both width and substrate. Streams and rivers with sand and gravel substrates were typically shallow, while the depth of mud-bottomed channels usually increased with width. A majority of the sites were shallow streams or rivers less than 3 feet (ca. 1 m) deep since it was possible to sample thoroughly such habitats. Stream bottom configurations varied from even with a uniform depth, to those with alternating shallow riffles and deeper pools. Mud and clay streams were usually of the former type as were channelized watercourses. Clayey streams, however, sometimes had riffles. Riffle-pool types were typically sand and gravel. Sampling bias may have been a problem since all types of streams were not sampled equally. However, quantitative sampling would not have been feasible either because certain types of streams predominated in different parts of the state, and some types were very uncommon.

Physiographic-Vegetation Zones.—Collecting sites were chosen in, and categorized according to, the state's major physiographic-vegetation areas (Bick, 1957; Louisiana Department of Natural Resources, 1974) (Fig. 1) to determine their effect on species distribution. Although the coastal marsh region (deltaic plain) was largely excluded because of unsuitable habitat, a few unproductive collecting attempts were made.

Drainage Basins.—Different types of streams were surveyed in each of the 12 drainage basins (Louisiana Department of Natural Resources, 1980) (Fig. 2) except for the Upper Mississippi River Basin, which is a very narrow strip of land inside the levees. These basin designations were used to categorize collecting sites to determine if the distribution of dryopoids is governed or influenced by watershed. Seagle and Hendricks (1979) stated that "with more attention being focused on dryopoids as indicators of water quality, it is becoming more important to know the distribution of this group within drainage basins." Other studies that examined this aspect of riffle beetle distribution include Sanderson and Brown (1959),

Brown (1960), and Finni et al. (1978).

The size, percentage of total land area, number of sites sampled, and percentage of total sites sampled for each basin are given in Table 2. Comparison of these percentages indicates the amount of effort expended in relation to land area. Some basins were relatively "over-sampled" (Lake Pontchartrain, Lower Mississippi, Pearl), while others were "under-sampled" (Atchafalaya, Barataria, Sabine). The Lake Pontchartrain and Pearl River basins were sampled extensively because they were the richest in species. Few samples were taken south of Lake Pontchartrain in the Lower Mississippi and Barataria basins because the deltaic area was generally unproductive for dryopoids. The Atchafalaya Basin was largely inaccessible except by boat.

Monthly Records.—Sampling was conducted throughout the year so that adult and larval presence could be documented. Unfortunately, it was not possible to expend the same amount of collecting effort on the same sites or sample them each month. Data representing the monthly records for the species are contained in Table 5; the amount of collecting effort per month is shown as a percentage of the total. It can be seen that effort, and hence probably results, is biased towards the summer months of June, July, and August during which 62% of the sampling was done.

Sampling Techniques

Because dryopoid beetles do not swim and are closely associated with the immediate substrate, microhabitats frequented by various species were sampled extensively. In this case, a microhabitat is defined as the particular substrate on which riffle beetles live. Seven major microhabitats were distinguished in Louisiana streams: gravel, root masses, waterlogged wood, allochthonous debris, vascular aquatic plants, aquatic moss, and rocks. Sand, alone or with small quantities of gravel, and mud were often sampled but found to be unproductive. Gravel nearly always was present in riffles; gravel in sandy streams was often found only beneath and downstream from a highway bridge or railroad bridge, indicating that it was not native. Submerged root masses of riparian vegetation were found along stream banks and most often in pools. These were either woody (willow, cypress, etc.) or herbaceous (grasses, emergent and shoreline plants). Debris, a combination of small sticks and leaf litter, was often found caught on snags in the current or layered in pools. Vascular aquatic plants were submerged (usually in the main current) or emergent (usually in pools and along banks), and included such genera as *Sparganium, Micranthemum, Potamogeton, Ludwigia, Alternanthera*, and *Polygonum*. The first 4 were often found in shallow, sunny riffles. Aquatic moss, usually *Fontinalis* spp., was only occasionally encountered on logs or other large objects in the main current or slower water near the shore. Rocks larger than gravel were rarely encountered during the study. Sometimes discarded concrete chunks were sampled. The only naturally rocky streams, with sandstone boulders, included in this study were located in southwest Natchitoches Parish. When possible, individual microhabitats were sampled separately, although combinations were sometimes unavoidable. All microhabitats available at a particular site were always sampled. Samples were also taken in both riffles and pools when these were present.

TABLE 2. Percentage and number of stream types, classified by major substrate component and mean width, sampled in the drainage basins of Louisiana from May 1979 to May 1981. Size and percentage of total land area are included for drainage basins.

BASIN % of Total (Size)	SAND			MUD			CLAY			GRAVEL			ROCK		% of Total (N)	# of Types
	%S[1]	%M[2] (N)	%L[3]	%S[1]	%M[2] (N)	%L[3]	%S[1]	%M[2] (N)	%L[3]	%S[1]	%M[2] (N)	%L[3]	%S[1]	%M[2] (N)		
ATCHAFALAYA 4.0% (1,810 Mi²)					50 (2)	25 (1)	25 (1)								2 (4)	3
BARATARIA 2.7% (1,200 Mi²)					50 (1)	50 (1)									1 (2)	2
CALCASIEU 9.1% (4,105 Mi²)	36 (5)	14 (2)	14 (2)	7 (1)	7 (1)		7 (1)	7 (1)	7 (1)						7 (14)	8
PONTCHARTRAIN 12.6% (5,700 Mi²)	19 (8)	33 (14)	7 (3)	2 (1)	7 (3)	2 (1)	10 (4)		2 (1)	10 (4)	2 (1)	5 (2)			22 (42)	11
MERMENTAU-VERMILION 14.8% (6,730 Mi²)	6 (1)	6 (1)		22 (4)	28 (5)	11 (2)	28 (5)								9 (18)	6
UPPER MISSISSIPPI 0.7% (325 Mi²)															0 (0)	0
LOWER MISSISSIPPI 2.4% (1,100 Mi²)	70 (7)	20 (2)									10 (1)				5 (10)	3
OUACHITA 24.3% (11,000 Mi²)	24 (10)	10 (4)		17 (7)	20 (8)	10 (4)	12 (5)			5 (2)	2 (1)				21 (41)	8
PEARL 2.0% (890 Mi²)	47 (8)	18 (3)	6 (1)							18 (3)	6 (I)	6 (1)			9 (17)	6

RED 17.2% (7,760 Mi²)	46 (16)	6 (2)		9 (3)	3 (1)		14 (5)	3 (1)		11 (4)	3 (1)		3 (1)	3 (1)	18 (35)	10
SABINE 6.3% (2,840 Mi²)	83 (5)			17 (1)											3 (6)	2
TERREBONNE 3.9% (1,750 Mi²)				17 (1)	33 (2)	17 (1)	17 (1)	17 (1)							3 (6)	5
% of Total (N)	31 (60)	14 (28)	3 (6)	9 (18)	12 (23)	5 (10)	11 (22)	2 (3)	1 (2)	7 (13)	3 (5)	2 (3)	<1 (1)	<1 (1)	(195)	

[1]0-20 ft (0-6 m) wide
[2]20-50 ft (6-15 m) wide
[3]50+ ft (15+ m) wide

Collecting techniques were adopted largely from those described by Musgrave (1935a), Brown and Shoemake (1964b), and Brown (1976). Branches and logs (wood) of a manageable size were removed from the water and searched; those too large to move were sampled *in situ* by rubbing or brushing the log surface while holding a net directly downstream to catch dislodged specimens. This same netting technique worked well when sampling aquatic plants and tree roots. In sand and gravel the net was held against the bottom while the substrate upstream was disturbed by foot (kick sampling). The net contents were searched in the net or after being placed in a large white enamel pan and allowed to partially dry. Upon drying, the normally sluggish beetles become more active and, therefore, more visible.

Sampling was not done quantitatively according to either a spatial or temporal scheme. A series of larval and adult dryopoids from each microhabitat was collected into separate, labeled vials of 95% ethyl alcohol. Genera with species difficult or impossible to identify in the field were collected in large series, while samples of rare or uncommon species included all individuals present. The number of specimens/species collected was recorded later when species identifications were completed. Samples of roots, plants, and debris were frequently brought back to the laboratory to be dried in a Berlese funnel. This technique sometimes yielded species that had been overlooked or were uncommon in field collections, especially in the genera *Dubiraphia* and *Microcylloepus* which are very small. A 15-watt, battery-powered, portable black light was used a few times for night collecting. Although some dryopoids are attracted to lights, the emphasis of this study was placed on in-stream collections so that associations between beetle populations and habitat could be determined.

Species Identification and Laboratory Procedure

Specimens were identified by the senior author using the literature and keys of Brown (1970, 1976), Hilsenhoff (1973), Musgrave (1935b), Sanderson (1938, 1953, 1954), and White (1978). When available, determined specimens were used for comparison. Verifications of species identifications were provided by Dr. Harley P. Brown at the University of Oklahoma, Norman. Counts were made of the total number of specimens/species collected.

Specimens heavily encrusted with debris were cleaned before examination with concentrated hydrochloric acid for about one minute as described by Hilsenhoff (1973), followed by an ultrasonic "bath" to remove loosened material. Most specimens were examined from alcohol since these were already relaxed and easier to manipulate, especially if genitalia dissections became necessary. However, some details such as granulation and punctation may be bolder when the specimen is at least partially dry.

When necessary for identification, especially in the genera *Stenelmis* and *Dubiraphia,* male genitalia were dissected and mounted. Most *Stenelmis* males can be distinguished from females by a ridge or bump on the inner surface of the middle tibia; otherwise, the tip of the penis can sometimes be seen protruding from the apex of the abdomen. Females have 2 genitalic structures, the styli, which often protrude. Genitalia were removed from specimens in the least destructive manner possible. Usually it was possible to extract the struc-

tures from the intact abdomen using fine-pointed pins; occasionally it was necessary to remove the abdomen first. The genitalia of *Stenelmis* spp. were each stored in a drop of glycerine in a microvial pinned beneath the specimen; those of *Dubiraphia* spp. were mounted on microscope slides with a water-soluble medium or placed in genitalia microvials.

Size ranges given in the text for all taxa except *Dubiraphia* spp. and problem species of *Stenelmis* are those of Brown (1976). The measurements of the known species of *Dubiraphia* are composites of Hilsenhoff's (1973) and our own, and are reported as elytral length only. All were made in dorsal view with a dry specimen. Total body length included the head, pronotum, and elytra; variability in the head position (extended or retracted) added additional variation to the measurement. Measurements of the male genitalia were made from the apex to the point where the penis and parameres join the basal lobe.

Representatives of species present at each site were mounted on card points and placed in the Louisiana State University Collection (LSUC) to serve as voucher specimens. Additional specimens were stored in rubber-stoppered vials containing 75% ethyl alcohol.

Additional Species Records

Collections of dryopoids made before and after this study, through June 1984, were examined and identified to supply possible additional records. These included specimens in the Louisiana State University Collection (LSUC) and a small collection from the University of Southwestern Louisiana (USL). These locality data are detailed in Appendix II and are cited in the species accounts and range maps. They are also included in Tables 3 and 4 (shown by asterisks) but are not figured into the frequency of collection percentages which are derived from the field study. Records of Harley P. Brown (HPB) at the University of Oklahoma are also occasionally cited (Brown, pers. com., Mar. 6 1979). Numbers in parentheses—i.e., (1), (2), etc.—following the locality name differentiate multiple collections.

Systematic Treatment

List of Louisiana Species

Family Psephenidae

Ectopria thoracica (Ziegler)

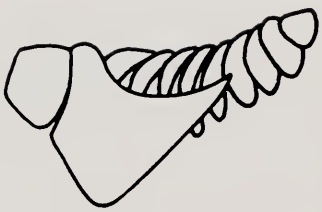
Family Dryopidae

Helichus basalis LeConte
Helichus fastigiatus (Say)
Helichus lithophilus (Germar)
Pelonomus obscurus LeConte

Family Elmidae

Ancyronyx variegata (Germar)
Dubiraphia brevipennis Hilsenhoff
Dubiraphia harleyi Barr
Dubiraphia parva Hilsenhoff ?
Dubiraphia vittata (Melsheimer)
Dubiraphia n. spp. A?, B?, C?
Gonielmis dietrichi (Musgrave)
Macronychus glabratus Say
Microcylloepus pusillus (LeConte)
Optioservus trivittatus (Brown)
Stenelmis antennalis Sanderson
Stenelmis bicarinata LeConte
Stenelmis convexula Sanderson
Stenelmis crenata (Say) ?
Stenelmis grossa Sanderson
Stenelmis lateralis Sanderson
Stenelmis sinuata LeConte
Stenelmis n. sp.

The basic anatomical terminology pertaining to adults, larvae, and genitalia used in this chapter is illustrated in Brown, 1976.



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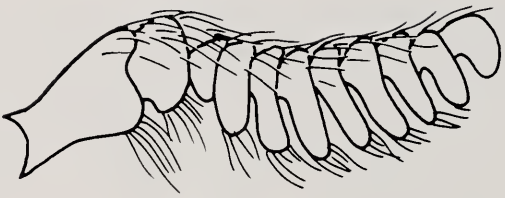

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7

Fig. 4. 1-2. Antennae of adult Dryopidae: 1, *Helichus;* 2, *Pelonomus obscurus.* 3-4. Antennae of adult Elmidae: 3, *Macronychus glabratus;* 4, *Stenelmis.* 5. Middle tibia of adult male *Stenelmis* (Elmidae), inner surface with ridge, lateral aspect. 6-7. Tarsi of adult *Stenelmis* (Elmidae), lateral aspect: 6, with last segment longer than previous 4 combined; 7, with last segment shorter than previous 4 combined.

Key to Adults of the Families and Species of Louisiana Dryopoidea

1 Typically soft-bodied; front coxae transverse and exserted with deep grooves posteriorly for reception of legs; elytra black; pronotum black medially, yellow or orange laterally; 3-5 mm long, 2-3 mm wide (Fig. 5.1); not aquatic, on vegetation near water: .... PSEPHENIDAE *Ectopria thoracica*

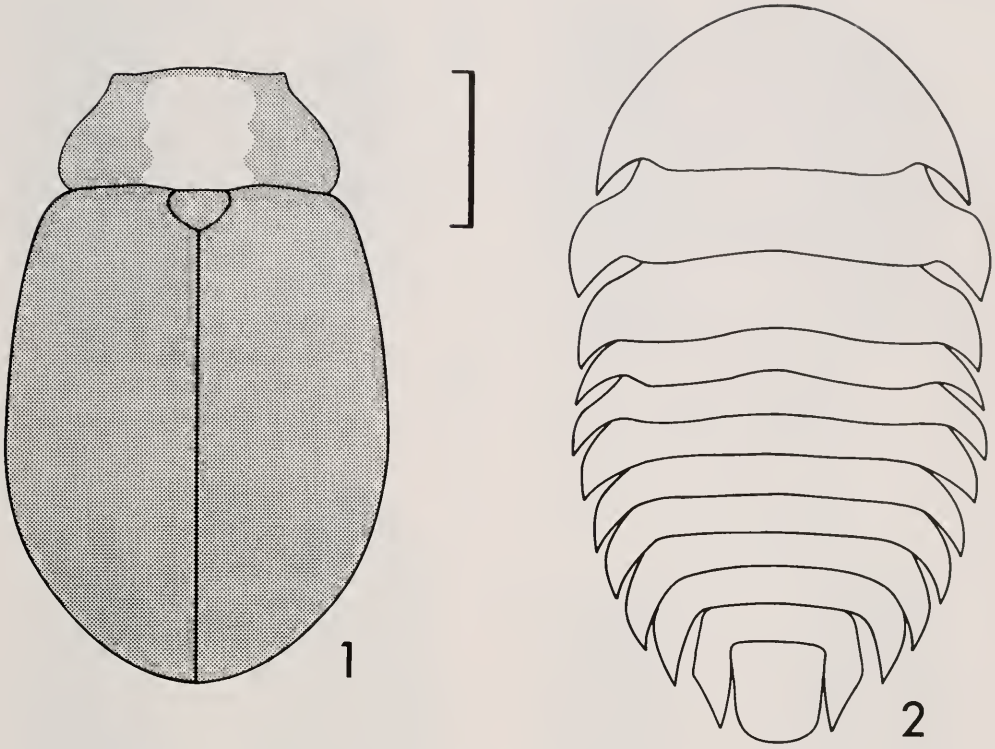

Fig. 5. 1-2. Psephenidae, *Ectopria thoracica:* 1, adult, pronotum and elytra, dorsal aspect; 2, larva, dorsal aspect. Scale bar = 1.0 mm.

Typically hard-bodied; front coxae rounded or transverse, not exserted; aquatic 2

2(1) Anterior coxae globular and without exposed trochantins; antennae usually filiform, not pectinate (Figs. 4.3, 4.4); less than 4 mm long: ..... ELMIDAE 6

Anterior coxae transverse and with exposed trochantins; antennae very short, 8 distal segments pectinate (Figs. 4.1, 4.2); more than 4 mm long: .... DRYOPIDAE 3

3(2) Second segment of antenna enlarged and heavily sclerotized, forming a triangular shield (Fig. 4.1); bases of antennae widely separated; head not prominent; body, excluding eyes and antennae, partly or completely covered with tomentum: ..... *Helichus* 4

Second segment of antenna not enlarged (Fig. 4.2); bases of antennae very close together; head prominent; entire body, including eyes and antennae, covered with short, erect pubescence; reddish to dark brown; 4.8-6.5 mm long, 2.0-2.5 mm wide (Fig. 6.4): .... *Pelonomus obscurus*

4(3) Dorsum uniformly covered

with fine, recumbent pubescence, without shiny sutural area except for scutellum; 4.4-5.8 mm long, 2.0-2.5 mm wide (Fig. 6.3): . *Helichus lithophilus*

Dorsum tomentose laterally with glabrous or sparsely pubescent shiny sutural area 5

5(4) First elytral stria faint, almost impunctate, at most with small punctures not extending to scutellum; hind coxa of male without ventrally-directed tooth-like process; brown to black; 4.3-5.5 mm long, 2.0-2.5 mm wide (Fig. 6.1): .... *Helichus basalis*

First elytral stria distinct, punctures larger and deeper, extending to scutellum; hind coxa of male with ventrally-directed tooth-like process; brown to black; 4.5-5.5 mm long, 2.2-2.5 mm wide (Fig. 6.2): .... *Helichus fastigiatus*

6(2) Hind coxae semi-globular and smaller than other coxae; posterior margin of prosternal process almost as wide as head 7

Hind coxae transverse and the same size or slightly larger than other coxae; posterior margin of prosternal process much narrower than head 8

7(6) Shiny dark brown or black with golden or silvery sublateral bands of tomentum; elytron with sublateral carina; antennae short, with 7 segments, apical segment enlarged (Fig. 4.3); 2.50-3.50 mm long, 1.00-1.30 mm wide (Fig. 7.6): .... *Macronychus glabratus*

Elytron black, conspicuously marked with C-shaped vitta and elongate apical spot, without sublateral carina; antennae filiform, with 11 segments; 2.10-

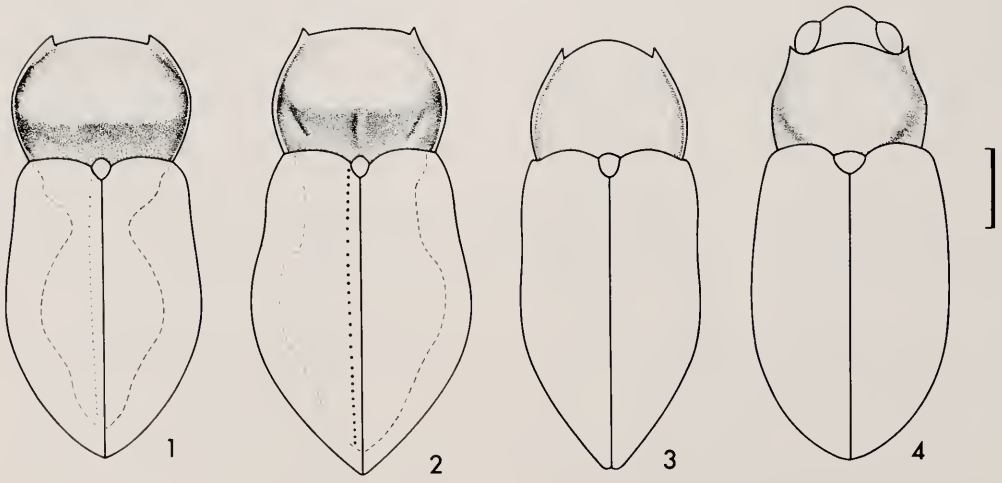

Fig. 6. 1-3. Adult Dryopidae, pronotum and elytra, dorsal aspect: 1, *Helichus basalis;* 2, *H. fastigiatus;* 3, *H. lithophilus.* 4. Adult Dryopidae, dorsal aspect, *Pelonomus obscurus.* Scale bar = 1.0 mm.

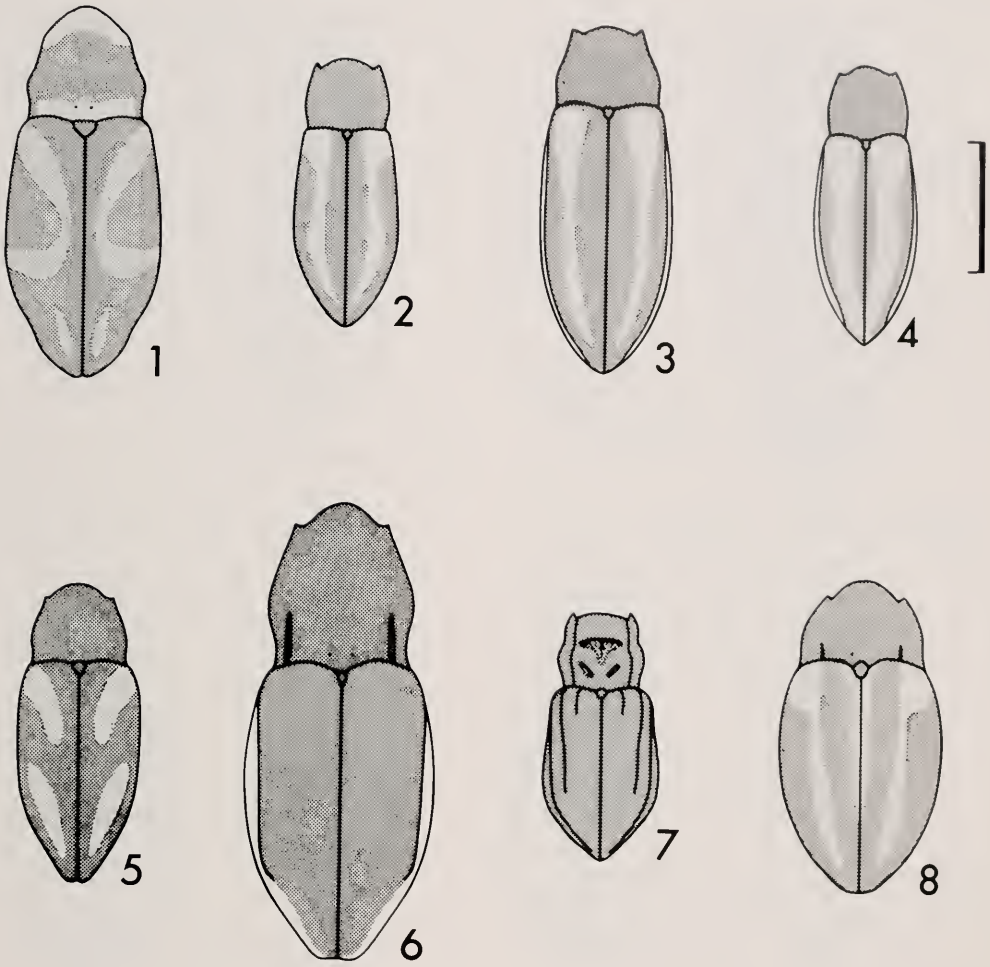

Fig. 7. 1-8. Adult Elmidae, pronotum and elytra, dorsal aspect: 1, *Ancyronyx variegata;* 2, *Dubiraphia brevipennis;* 3, *D. harleyi;* 4, *D. vittata;* 5, *Gonielmis dietrichi;* 6, *Macronychus glabratus;* 7, *Microcylloepus pusillus;* 8, *Optioservus trivittatus.* Scale bar = 1.0 mm.

2.60 mm long, 0.90-1.10 mm wide (Fig. 7.1): .... *Ancyronyx variegata*

8(6) Anterior tibia without fringe of tomentum; males of most species with swelling or ridge on inner surface of each middle tibia (Fig. 4.5); elytron immaculate, vittate, or with vitta broken into humeral and apical spots: ..... *Stenelmis* 9

Anterior tibia with medial fringe of tomentum; males without swelling or ridge on inner surface of each middle tibia; elytral characters variable 16

9(8) Surface of femur punctate, not granulate; lateral processes on penis subangulate anteriorly (Fig. 9.5); elytron bimaculate, often faintly; 3.25-3.60 mm long, 1.25-1.40 mm wide (Fig. 8.5): ..... *Stenelmis grossa*

Surface of femur granulate; lateral processes on penis, if present, rounded; elytron variable 10

10(9) Elytral vitta broad, covering umbone at humeral angle and nearly all of space between first stria and sixth interval; 2.65-3.00 mm long, 0.95-1.10 mm wide (Figs. 8.6, 9.6): .... *Stenelmis lateralis*

Elytral vitta or humeral spot narrower, inside sixth interval and not covering umbone 11

11(10) Antenna bicolored, distal segments black and basal 3-6 segments testaceous; elytron with distinct vitta or maculae; 2.50-2.70 mm long, 1.00 mm wide (Figs. 8.1, 9.1): .... *Stenelmis antennalis*

Antenna testaceous, not bicolored; elytron variable 12

12(11) Last tarsal segment shorter than previous 4 combined (Fig. 4.7); body robust; in dorsal view, lateral margins of pronotum in anterior third slightly rounded and either parallel or angled anteromedially, appearing to clasp head; 3.30-3.70 mm long, 1.25-1.50 mm wide (Figs. 8.4, 9.4): ... *Stenelmis crenata*?

Last tarsal segment slightly or distinctly longer than previous 4 combined (Fig. 4.6); other characters variable 13

13(12) Penis without lateral processes (Fig. 9.8); ridge or bump present on middle tibia of male; elytron distinctly or faintly vittate, bimaculate, or immaculate; 2.50-2.80 mm long, 0.90-1.00 mm wide (Fig. 8.8): ..... *Stenelmis* n. sp.

Penis with rounded or elongate lateral processes (Figs. 9.2, 9.3, 9.7); middle tibia of male with or without ridge; elytron usually bimaculate, often faintly; 2.85-3.70 mm long, 1.00-1.50 mm wide 14

14(13) Middle tibia of male with ridge; penis with widely rounded lateral processes (Fig. 9.3); body appearing convex and smooth; elytral striae, pronotal tubercles and sulcus not prominent; 3.09-3.64 mm long, 1.21-1.44 mm wide (Fig. 8.3): ..... *Stenelmis convexula*

Middle tibia of male without ridge; penis with narrowly rounded lateral processes (Figs. 9.2, 9.7); body not appearing convex and smooth; elytral striae, pronotal tubercles and sulcus prominent 15

15(14) Lateral margins of pronotum strongly divergent in anterior third, resembling loose collar behind head; elytral striae with large, deep punctures; tubercles of pronotum very prominent, basal tubercle carinate; 3.20-3.45 mm long, 1.20-1.35 mm wide (Figs. 8.7, 9.7): ..... *Stenelmis sinuata*

Lateral margins of pronotum parallel or weakly divergent in anterior third; elytral striae with punctures

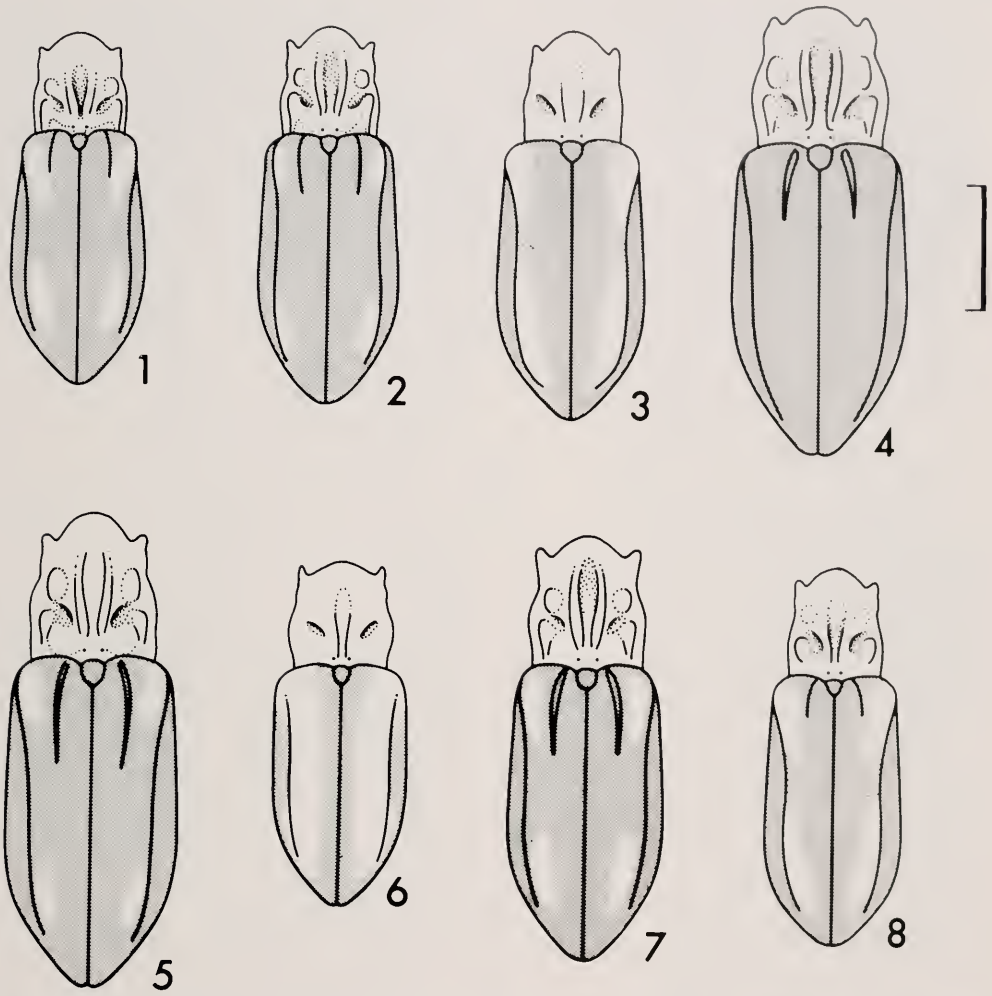

Fig. 8. 1-8. Adult Elmidae, *Stenelmis*, pronotum and elytra, dorsal aspect: 1, *S. antennalis;* 2, *S. bicarinata;* 3, *S. convexula;* 4, *S. crenata*?; 5, *S. grossa;* 6, *S. lateralis;* 7, *S. sinuata;* 8, *Stenelmis* n. sp. Scale bar = 1.0 mm.

not so large and deep; tubercles of pronotum not as prominent, basal tubercle not carinate; 2.94-3.46 mm long, 1.05-1.32 mm wide (Figs. 8.2, 9.2): .... *Stenelmis bicarinata*

16(8) Pronotum with sublateral carinae for entire length or present in basal third only 17

Pronotum without sublateral carinae 18

17(16) Pronotum with 2 longitudinal carinae and transverse impression anterior to middle; body pitted and ridged, brown to black; elytron unmarked, bimaculate, or vittate; 1.65-2.20 mm long, 0.68-0.90 mm wide (Fig. 7.7): .... *Microcylloepus pusillus*

Pronotum with 2 short basal carinae and no transverse impression; body rather

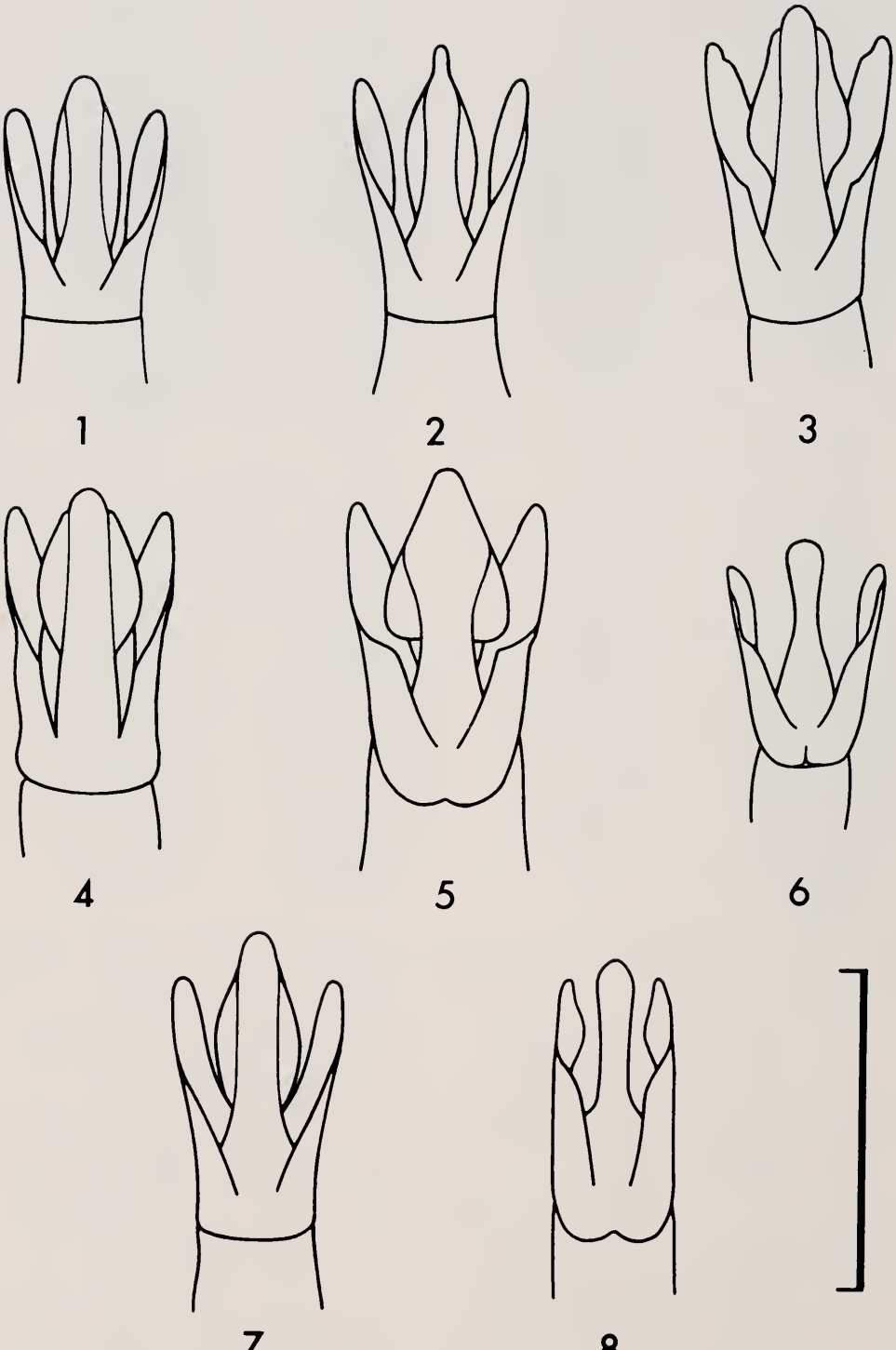

Fig. 9. 1-8. Adult Elmidae, *Stenelmis*, male genitalia, dorsal aspect: 1, *S. antennalis;* 2, *S. bicarinata;* 3, *S. convexula;* 4, *S. crenata*?; 5, *S. grossa;* 6, *S. lateralis;* 7, *S. sinuata;* 8, *Stenelmis* n. sp. Scale bar = 0.5 mm.

smooth and convex, dark brown; each elytron with both sutural and medial vittae; 1.69-2.19 mm long, 0.78-1.14 mm wide (Fig. 7.8): ..... *Optioservus trivittatus*

18(16) Elytron black with 2 oblique yellow or testaceous spots; legs black with yellow tibiae; 2.0-2.6 mm long, 0.95-1.10 mm wide (Fig. 7.5): ..... *Gonielmis dietrichi*

Elytron black or dark brown with an entire longitudinal vitta or with vitta broken into 2 spots: .. *Dubiraphia* 19

19(18) Penis usually longer than 0.31 mm 20

Penis usually shorter than 0.31 mm 21

20(19) Penis measuring 0.31-0.37 mm, abruptly narrowed at apical third to half or evenly tapered; elytron vittate, vitta covering 3-4 intervals at widest point posterior to humerus; elytron 1.25-1.40 mm long: ..... *Dubiraphia parva*?

Penis measuring 0.39-0.45 mm, narrow and evenly tapered to tip (Fig. 10.2); elytron vittate, vitta covering 1 1/2 to 2 1/2 intervals at widest point posterior to humerus; elytron 1.65-2.02 mm long (Fig. 7.3): . ..... *Dubiraphia harleyi*

21(19) Elytron 1.04-1.28 mm long, vitta or apical macula covering 2 intervals at widest point posterior to humerus; penis 0.22-0.28 mm long; femur light, only slightly darker than tibia and tarsus: .... *Dubiraphia* n. sp. C?

Elytron usually longer than 1.29 mm; other characters variable 22

22(21) Elytral vitta or apical macula narrow, covering 1 to 3 intervals at widest point posterior to humerus 23

Elytral vitta or apical macula wide, covering 4 to 5 intervals at widest point posterior to humerus 24

23(22) Penis stout, width 2 to 2 1/2 times width of paramere at midlength, tip broadly rounded; femur and tibia darker than tarsus; elytron 1.33-1.57 mm long: .....

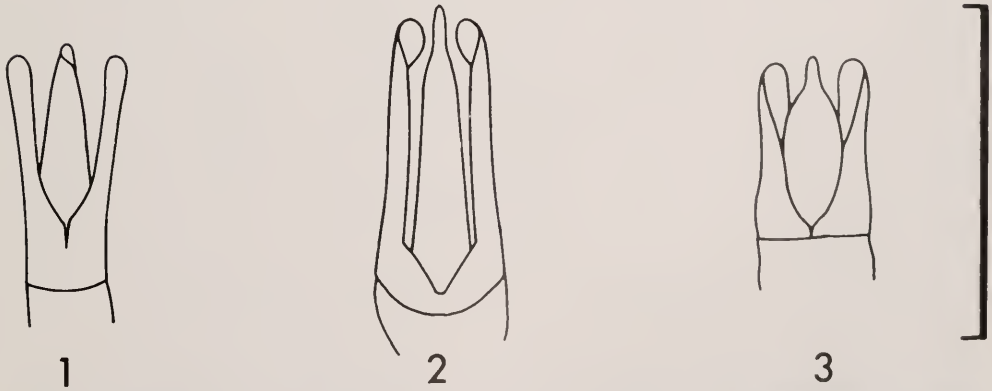

Fig. 10. 1-3. Adult Elmidae, *Dubiraphia,* male genitalia, dorsal aspect: 1, *D. brevipennis;* 2, *D. harleyi;* 3, *D. vittata.* Scale bar = 0.5 mm.

..... *Dubiraphia* n. sp. B?

Penis narrower, width no more than 1/2 times width of paramere at midlength, tip narrowly rounded (Fig. 10.1); femur bicolored, dark basally and light apically, or entirely dark; tibia and tarsus light; elytron 1.30-1.53 mm long (Fig. 7.2): ... *Dubiraphia brevipennis*

24(22) Penis stout, at least 2 times width of paramere at midlength, sides convex to near distinctly narrowed tip (Fig. 10.3); elytron vittate or occasionally bimaculate; palpi testaceous like antennae or darker; elytron 1.30-1.83 mm long (Fig. 7.4): .. *Dubiraphia vittata*

Penis narrow, 1 1/2 to 2 times width of paramere at midlength, sides straight to tip; elytron vittate; palpi testaceous; elytron 1.38-1.55 mm long: .....
..... *Dubiraphia* n. sp. A?

Key to Larvae of the Families and Genera of Louisiana Dryopoidea

1 Broadly ovoid in shape and very flat; lateral margins of each segment greatly expanded; head completely concealed dorsally by pronotum (Fig. 5.2): ..
.... PSEPHENIDAE *Ectopria*

Less broad and flat, usually slender, round or triangular in cross-section; head exposed in dorsal view (Figs. 11.1-11.6): .....
..... ELMIDAE 2

2(1) Last abdominal segment very long and slender, at least 4 times longer than wide; operculum confined to posterior third of this segment (Fig. 11.2): . *Dubiraphia*

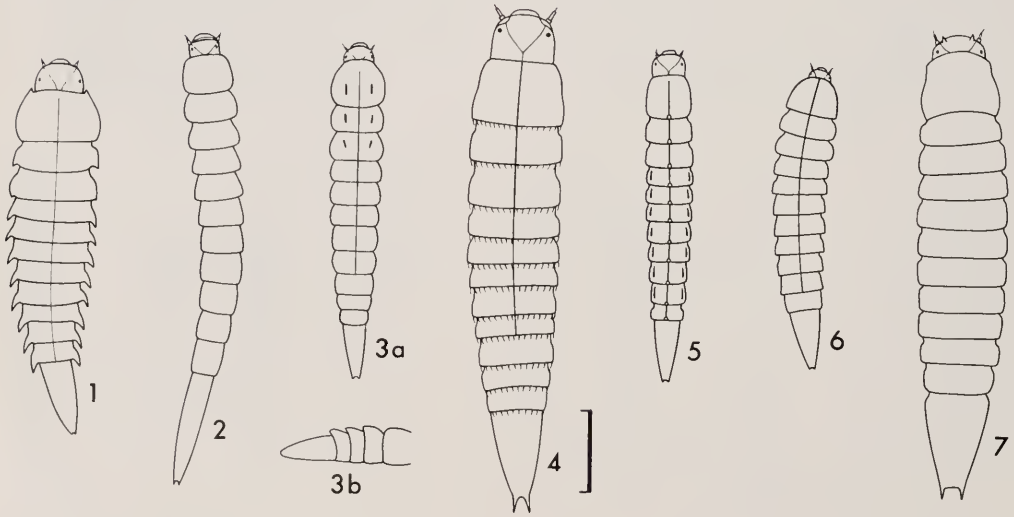

Fig. 11. 1-7. Larval Elmidae: 1, *Ancyronyx*, dorsal aspect; 2, *Dubiraphia*, dorsal aspect; 3, *Gonielmis*, a, dorsal aspect, b, lateral aspect, distal segments; 4, *Macronychus*, dorsal aspect; 5, *Microcylloepus*, dorsal aspect; 6, *Optioservus*, dorsal aspect; 7, *Stenelmis*, dorsal aspect. Scale bar = 1.0 mm.

Last abdominal segment not especially long or slender, less than 4 times longer than wide; operculum not confined to posterior third 3

3(2) Prothorax with posterior sternum so that procoxal cavities are closed posteriorly 4

Prothorax without posterior sternum so that procoxal cavities are open posteriorly 6

4(3) Posterolateral margins of abdominal segments 1-8 produced into hooked or toothed processes; body rather robust (Fig. 11.1): ..... *Ancyronyx*

Posterolateral margins of abdominal segments without such processes; body elongate or robust 5

5(4) Apical abdominal segment with 2 prominent posterolateral spines; narrow mid-dorsal stripe, if present, not enlarged into spots at posterior margin of each sclerite; color light to dark brown (Fig. 11.7): .. *Stenelmis*

Apical abdominal segment without posterolateral spines; narrow mid-dorsal stripe enlarged into spots at posterior margin of each sclerite; color dark brown to black (Fig. 11.5): ..... *Microcylloepus*

6(3) Mesopleuron composed of one part; pronotum expanded laterally, appearing hood-like; body triangular in cross-section, rather robust (Fig. 11.6): ..... *Optioservus*

Mesopleuron composed of 2 parts; pronotum not expanded laterally; body variable 7

7(6) Abdominal segments 1-6 with pleura, not humped dorsally, each with a posterior fringe of hairs; last abdominal segment with 2 long, narrowly separated apical spines (Fig. 11.4): ..... *Macronychus*

Abdominal segments 1-7 with pleura, humped dorsally and bearing conspicuous scale-like hairs; last abdominal segment slightly emarginate at apex, not spined (Fig. 11.3): ..... *Gonielmis*

Survey of Louisiana Taxa

Superfamily Dryopoidea

Dryopoid affinities and characteristics were examined by Crowson (1955) who classified the superfamily in the Suborder Polyphaga, Series Dascilliformia, along with the Dascilloidea, Byrrhoidea, Buprestoidea, Rhipiceroidea, Elateroidea, and Cantharoidea. Arnett (1960) placed the Dryopoidea in the Series Elateriformia and excluded the Dascilloidea from the group. A phylogeny of the Dryopoidea based on Hennig's principles of phyletic classification was proposed by Crowson in 1978; he retained the Dryopoidea within the Series Elateriformia along with the Byrrhoidea, Elateroidea, Cantharoidea, and Artematopoidea. According to Crowson (1955), the dryopoids probably arose from common stock with the dascilloids and byrrhoids and may have been ancestral to the buprestoids, rhipiceroids, and elateroids. Ancestral Dryopoidea have been traced to the early Jurassic

Period, and it is likely that the evolutionary bifurcations resulting in our modern families were completed early in the Cretaceous Period (Crowson, 1978).

Synoptic works on the Dryopoidea were published by LeConte (1852) and Horn (1870) under the name Parnidae and included genera now placed in the families Psephenidae, Dryopidae, Elmidae, and Limnichidae. LeConte introduced a new criterion for identification based on tarsal structure, divided the family into 3 groups (Eurypalpini, Dryopini, Elmini), added a genus (*Eurypalpus* = *Psephenus*) previously assigned to another family, and provided Latin descriptions and English notes for several species. In a similar synoptic paper LeConte (1853) examined genera in the family Atopidae which are now placed in the Psephenidae and Ptilodactylidae. Horn (1870) proposed a classification based on LeConte's work which divided the Parnidae into the subfamilies (*sic*) Psephenidae, Parnidae, and Elmidae. The paper included keys to the subfamilies, tribes, genera, and species and a description and discussion of each species.

Hinton (1939b) revised the systematics of the group by elevating the Dryopidae (=Parnidae) to superfamily status and naming the Psephenidae, Dryopidae, Elmidae, and Limnichidae (formerly in Byrrhidae) as families, thus forming the basis for our modern classification. This extensive taxonomic-morphological paper presented detailed descriptions and comparisons of the internal and external anatomy of larvae, pupae, and adults to support these revisions.

In his work on the Coleoptera, Crowson (1955) included 8 families in the Dryopoidea: Chelonariidae, Dryopidae, Elmidae, Eurypogonidae, Heteroceridae, Limnichidae, Psephenidae, and Ptilodactylidae. In 1978 he added Eulichidae (formerly in Ptilodactylidae) to the list and excluded the Eurypogonidae which he had placed in a new superfamily, Artematopoidea, in 1973. Arnett (1960, 1962) listed 7 families, placing the Eurypogonidae and most of the genera now included in Psephenidae and Ptilodactylidae in the Dascillidae. According to Borror et al. (1981), the superfamily is composed of 10 families, those of Arnett plus Callirhipidae, Brachypsectridae, and Artematopidae (=Eurypogonidae).

The aquatic dryopoids of the United States, including members of the families Chelonariidae, Dryopidae, Elmidae, Limnichidae, Psephenidae, and Ptilodactylidae, were treated in a comprehensive work by Brown (1976). Introductory information on collection, preservation, and anatomy was included along with illustrated adult and larval keys and notes on habitat and distribution of species. Brown (1981b) later presented corrections and additions to update his manual. The Chelonariidae were recently removed from the list of aquatic dryopoids because the larvae were found to be terrestrial (Spangler, 1980). In another paper Brown (1975a) illustrated the distributions of dryopoid and dascilloid genera in the United States. The larval morphology of the Dryopidae, Elmidae, and Limnichidae, treated as subfamilies of Dryopidae, was studied at the generic level by Bertrand (1955, 1965) and West (excluding Limnichidae) (1929b).

Crowson (1955) stated that aquatic adaptations in the Dryopoidea seem to be "basic" in the larvae rather than in the adults, the opposite of the situation in the Hydrophiloidea. The most characteristic adaptations of dryopoid larvae are retractile tracheal gills in the rectum or ninth abdominal segment cov-

ered by a ventral operculum. Although terrestrial larvae often lack gills and opercula, they usually can be recognized by well-developed, articulated, setose mandibular prosthecae and a free labrum. Dryopoid adults are more difficult to characterize since they often have features in common with the byrrhoids, dascilloids, and/or rhipiceroids. Crowson claimed that adults usually possess one or more of the following characteristics: "crenulate hind margin of the pronotum, distinct transverse suture in the metasternum, distinct frontoclypeal suture, last tarsal segment as long as rest together, middle or hind coxae separated."

As a result of this present study, aquatic members of the families Psephenidae, Dryopidae, and Elmidae have been found to occur in Louisiana. Although the state has several terrestrial species of Limnichidae and Ptilodactylidae, aquatic species of these families are apparently very rare or absent.

Family Psephenidae Lacordaire, 1854

Psephenid adults are characterized by being typically soft-bodied and depressed with the mandibles concealed and the labrum invisible anteriorly. Larvae, commonly called water pennies, are round or oval (onisciform) and very flat with the head concealed by expanded pronotal margins. While the larvae are strictly aquatic, adults generally do not enter the water except to oviposit (Brown, 1976).

Distributed worldwide, Psephenidae is a small family with 17 North American representatives in 6 genera (Brigham, 1981; Brown, 1981a, 1983a). Larvae of the 3 subfamilies Eubrianacinae, Psepheninae, and Eubriinae are separable on the basis of gill, opercular, and abdominal sclerite characteristics. The Eubrianacinae is comprised of one western species, *Eubrianax edwardsii* (LeConte). Six of the 7 species of Psepheninae are also western. The genus *Psephenus* was revised by Brown and Murvosh in 1974. The ecology of *Psephenus herricki* (DeKay), the widespread eastern species, has been studied by Murvosh (1970). Although this species has been reported from the nearby states of Arkansas, Mississippi, and Alabama, it has not been collected and probably does not occur here since Louisiana is located entirely south of the Fall Line (Murvosh, 1970).

Five of the 9 North American species of Eubriinae are eastern, only one of which is widespread. Larval eubriines, commonly called false water pennies, are distinguished by the absence of abdominal gills except for 3 tufts enclosed in an operculate chamber on the ninth abdominal segment. According to Brigham (1981), this group should be given family status. In the past, Eubriinae was usually placed in the family Dascillidae on the basis of adult characters (Arnett, 1962). Larval Eubriinae were thought to be larval dryopids (e.g., *Helichus*) until reared by Bertrand (1939). This error is carried in a number of publications including Peterson (1967) and Pennak (1978). The subfamily was reviewed briefly by Brown (1980) in a paper that described a new species, *Alabameubria starki,* from larvae collected in Alabama. The group, treated as a family (Eubriidae), was also discussed by Brigham (1981). A catalog of the Psephenidae was recently published (Brown, 1983a).

There are few studies of the group at the family level. The respiratory adaptations, biology, and taxonomy of the psephenids were examined by Hinton (1955) in a paper which emphasized anatomical and morphological charac-

teristics. General treatment of the family is included in Brown's (1976) aquatic dryopoid manual.

Genus *Ectopria* LeConte, 1853

Ectopria larvae are distinctively flattened dorso-ventrally and are oval in outline with the lateral margins of each body segment greatly expanded. The pronotum completely conceals the head from dorsal view. Gills are caudal and retractile into an operculate chamber; external, ventral abdominal gills are absent. Larvae cannot be identified to species (Brigham, pers. com., Mar. 22 1984).

The genus may be restricted to the New World with 3 Nearctic and 4 Neotropical species (Brigham, 1981; Brown, 1981a). In 1981 Brigham described a new eastern United States species, *Ectopria leechi*, resurrected *E. thoracica* (Ziegler), and provided a key to separate the 3 Nearctic species. The life history of *Ectopria nervosa* was studied by Schafer (1950). *Ectopria* is the only psephenid known to occur in Louisiana.

Ectopria cf. *E. thoracica* (Ziegler)
Figs. 5.1, 5.2; Map, Fig. 12

Eubria thoracica Ziegler, 1844, *Proc. Acad. Nat. Sci. Phila.* 2:269.

DIAGNOSTIC DESCRIPTION: ADULTS—Not aquatic; see Fig. 5.1 and key. LARVAE—See Fig. 5.2.

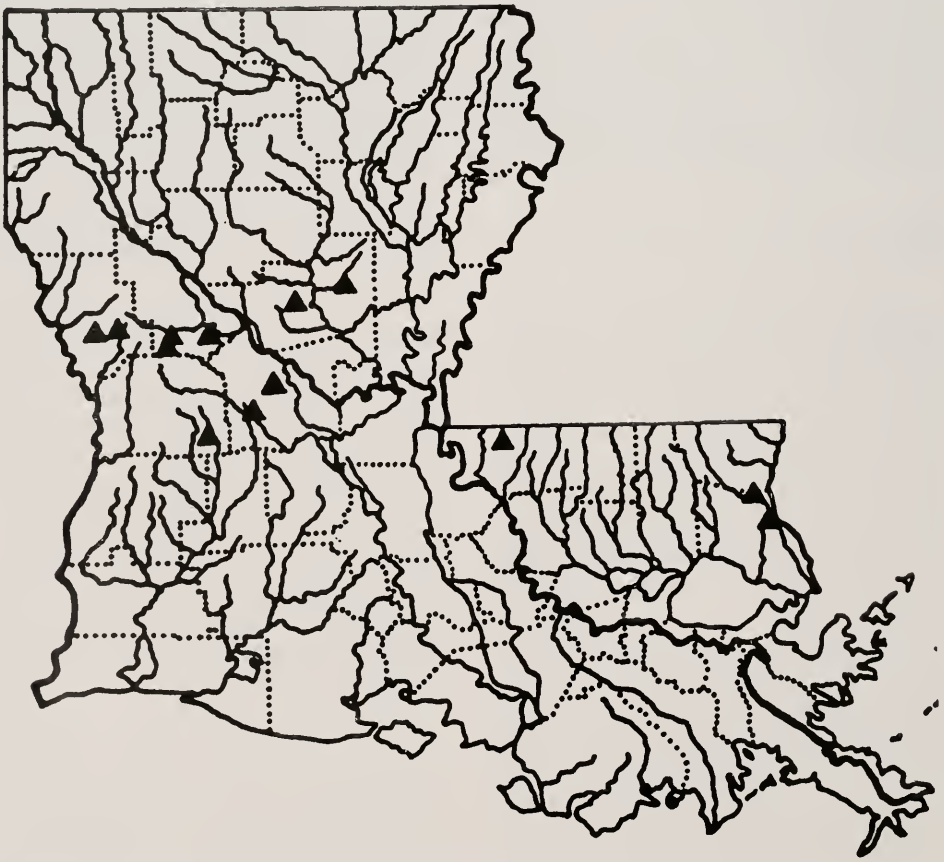

Fig. 12. The known distribution of Psephenidae, *Ectopria thoracica*, in Louisiana.

COMMENTS: The flattened, oval-shaped larvae of the family are distinctive. The concealed head and antennae separate psephenid larvae from members of other aquatic beetle families. An *Ectopria* larva may be distinguished from *Psephenus herricki*, the widespread eastern water penny, by its lack of external abdominal gills. Although *E. thoracica* and *E. nervosa* occur sympatrically, the latter species is very uncommon. Only adult *E. thoracica* have been collected at black light in Louisiana. Our larval specimens are almost certainly *E. thoracica* despite the fact that larvae cannot be determined to species (Brigham, pers. com., Mar. 22 1984) and will be referred to as such in the text and tables. The following records are for larvae, unless otherwise indicated.

SPECIMENS EXAMINED: 5 adults, 28 larvae.

GEOGRAPHIC RANGE: Entire eastern North America from Quebec and Ontario to Florida, west to Iowa, Missouri, Oklahoma, and Louisiana (Barr, 1981; Brigham, pers. com., Mar. 22 1984; Brown, 1983c).

DISTRIBUTION IN LOUISIANA: Scattered locations in the central, east-central, west-central, and southeastern ("Florida parishes") parts of the state. Occurs in the following drainage basins: Calcasieu River, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Ouachita River, Pearl River, Red River, and Sabine River (Fig. 12).

LOUISIANA RECORDS: GRANT P.—Gray Branch; LA SALLE P.—Trout Creek; NATCHITOCHES P.—Bayou Pierre, Kisatchie Bayou, Kisatchie Bayou Campgrd. (adult) (LSUC), Little Bayou Pierre, Little Bayou Pierre (adults) (LSUC), Little Bayou Pierre (HPB); RAPIDES P.—Castor Creek, Spring Creek; SABINE P.—Lewing Creek, 6 mi W of Florien (adult) (LSUC); ST. TAMMANY P.—Mill Creek, Talisheek Creek (2); VERNON P.—Sixmile Creek; WEST FELICIANA P.—West Fork Thompson Creek.

HABITAT: Primarily in small- to medium-sized sandy streams, occasionally in clay-bottomed creeks. Found on a variety of substrates including wood, moss, roots, gravel, and rock.

Family Dryopidae Erichson, 1847

Adult dryopids, aquatic or riparian, are distinguished by hard bodies, distinctive short antennae with last 8 segments typically pectinate, transverse anterior coxae with exposed trochantins, non-retractile legs, and 5 tarsal segments. They are often called long-toed water beetles because of their long tarsal claws. The terrestrial larvae are cylindrical (elateroid) with reduced abdominal sternites and pleurites, and without retractile gills and opercula.

The dryopid fauna of America north of Mexico is composed of 12 species in the genera *Dryops, Helichus,* and *Pelonomus* (Brown, 1981a, 1983b). Four of the 6 primarily eastern species in the latter 2 genera occur in Louisiana.

There are few comprehensive treatments of the Dryopidae at the family level. Brown (1970) published a key to the New World genera with comments on their occurrence. The family is most thoroughly covered in Brown (1976).

Genus *Helichus* Erichson, 1847

Adult beetles in the genus *Helichus* are characterized by their widely separated, pectinate antennae, the second segment of which is expanded into a heavily sclerotized triangular shield (Fig. 4.1). The terrestrial larvae were most recently described by Ulrich (1986).

Species of *Helichus* occur in North and South America and the Old World. This is the largest dryopid genus in North America with 10 species; 3 of the 4 eastern species are found in Louisiana. A synopsis of the genus with a key, species descriptions, and illustrations of male genitalia was published by Musgrave (1935b). Hinton described 4 new species in 1935 (1935a), and in 1937 commented on several errors in Musgrave's (1935b) paper and proposed corrections. One of the species discussed was *H. fastigiatus* (Say) which occurs in Louisiana. Nelson (1981) noted taxonomic problems and errors existing within the genus and proposed solutions. He is currently working on a revision.

Helichus basalis LeConte, 1852
Fig. 6.1; Map, Fig. 13.1

Helichus basalis LeConte, 1852, *Proc. Acad. Nat. Sci. Phila.* 6:43.

DIAGNOSTIC DESCRIPTION: ADULTS—Brown to black; thorax depressed behind middle; elytron with bronze tomentum laterally, usually with shiny glabrous to sparsely pubescent sutural area widest basally and narrowed apically, rarely pubescent medially; each elytral stria indistinct, with small shallow punctures becoming impunctate near base; first stria not extending to scutellum (Fig. 6.1); male genitalia with slender, acutely-pointed parameres; 4.3-5.5 mm long, 2.0-2.5 mm wide. LARVAE—Not aquatic.

COMMENTS: Adult males and females may be confused with *H. fastigiatus* females, but they differ by having shallower elytral punctures with the first elytral stria not reaching the scutellum. There is considerable variation in the amount of medial "rubbing" present on the elytral disk, ranging from bare to sparsely pubescent.

SPECIMENS EXAMINED: 199 adults.

GEOGRAPHIC RANGE: Entire eastern North America from Quebec to Georgia, west to Kansas and eastern Texas (Brown, 1976, 1983c; LeSage and Harper, 1975). Louisiana records may be the most southern for the species.

DISTRIBUTION IN LOUISIANA: Northwestern, north-central, west-central, and southeastern (northwestern "Florida parishes") areas of the state; absent from the southwestern prairie and the alluvial and deltaic plains. Occurs in the following drainage basins: Calcasieu River, Lake Pontchartrain, Lower Mississippi River, Ouachita River, Red River, and Sabine River (Fig. 13.1).

LOUISIANA RECORDS: ALLEN P.—Soapstone Creek; BIENVILLE P.—Cypress Creek, Redfield Branch, NE Bienville (HPB), SE Arcadia (HPB); BOSSIER P.—trib. Little Cypress Bayou; CADDO P.—Cypress Bayou, Shettleworth Bayou; CALDWELL P.—trib. Flat Creek; CATAHOULA P.—Haggerty Creek; CLAIBORNE P.—Middle Fork Bayou d'Arbonne; DE SOTO P.—Bull Bayou; EAST FELICIANA P.—Foster Creek, Hurricane Creek, Little Comite Creek (LSUC), Sandy Creek (1,2), Sandy Creek (HPB), Woodland Creek; GRANT P.—Nantachie Creek; JACKSON P.—trib. Edwards Branch; LINCOLN P.—trib. Choudrant Creek; NATCHITOCHES P.—Antoine Creek, Bayou Pierre; RAPIDES P.—Germany Branch (HPB), Hemphill Creek; RED RIVER P.—trib. Black Lake Bayou, trib. Brushy Creek; SABINE P.—Lewing Creek; VERNON P.—Calcasieu River; WEST FELICIANA P.—Bayou Sara, Tunica Bayou, West Fork Thompson Creek; WINN P.—E trib. Kiesche Creek, Mill Creek.

HABITAT: Small- to medium-sized streams with sand, gravel, or rarely clay substrates. Most often collected on roots, wood, or gravel.

Helichus fastigiatus (Say, 1824)
Fig. 6.2; Map, Fig. 13.2

Parnus fastigiatus Say, 1824, Appendix Vol. II, Keating's Expedition to Source of St. Peter's River Under Major Long, p. 275.

DIAGNOSTIC DESCRIPTION: ADULTS —Brown to black; thorax depressed behind middle; elytron with bronze tomentum laterally, and shiny glabrous to sparsely pubescent sutural area widest basally and narrowed apically; each elytral stria very distinct, with large punctures even near base; first stria extending to scutellum (Fig. 6.2); hind coxa of male with prominent ventrally-directed, tooth-like process; male genitalia with stout, blunt-tipped parameres; 4.5-5.5 mm long, 2.2-2.5 mm wide. LARVAE—Not aquatic.

COMMENTS: The characteristic hind coxal teeth of the male are best seen in lateral view. The female is distinguished from both sexes of *H. basalis* by the presence of very distinct elytral striae, the first of which extends to the scutellum. The size of the dorso-medial bare to sparsely pubescent elytral area varies among individuals.

SPECIMENS EXAMINED: 24 adults.

GEOGRAPHIC RANGE: Entire eastern North America from New Brunswick and Quebec to Florida, west to eastern Kansas and Oklahoma, and north to Illinois (Brown, 1983c; LeSage and Harper, 1975).

DISTRIBUTION IN LOUISIANA: Scattered localities in the north-central and southeastern (northern "Florida parishes") areas of the state; absent from the southwestern prairie and the alluvial and deltaic plains. Occurs in the following drainage basins: Lake Pontchartrain, Lower Mississippi River, Ouachita River, Pearl River, and Red River (Fig. 13.2). This species is much less common than either *H. basalis* or *H. lithophilus* (Germar).

LOUISIANA RECORDS: BIENVILLE P.—Redfield Branch, NE Bienville (HPB); CATAHOULA P.—trib. Birds Creek; EAST FELICIANA P.—Hurricane Creek, Woodland Creek; GRANT P.—Gray Branch; JACKSON P.—trib. Edwards Branch; LA SALLE P.—Doyle Branch; RAPIDES P.—Loving Creek (USL); RED RIVER P.—trib. Brushy Creek; WASHINGTON P.—Bogue Chitto River, Bogue Lusa Creek, Bonner Creek, Crains Creek, Hays Creek (USL), North Carson Creek; WEST FELICIANA P.—Tunica Bayou.

HABITAT: Small- to medium-sized streams with sand and/or gravel substrates. Most often collected on wood or roots.

Helichus lithophilus (Germar, 1824)
Fig. 6.3; Map, Fig. 13.3

Elmis lithophila Germar, 1824, *Insectorum Species Novae aut Minus Cognitae, Descriptionibus Illustratae,* p. 88.

DIAGNOSTIC DESCRIPTION: ADULTS—Golden-brown to dark brown; thorax not depressed behind middle; body uniformly covered with fine, silky pubescence except for shiny scutellar area; each elytral stria composed of small, barely visible punctures (Fig. 6.3); male genitalia very long and slender; 4.4-5.8 mm long, 2.0-2.5 mm wide. LARVAE—Not aquatic.

COMMENTS: This species is unlikely to be mistaken for either *H. basalis* or *H: fastigiatus.* Specimens appear glossy and more streamlined, without distinct elytral striae or dorsal "rubbed" patches.

SPECIMENS EXAMINED: 277 adults.

GEOGRAPHIC RANGE: Entire eastern North America from Quebec and Ontario to Florida, west to eastern Kansas, Oklahoma, and Texas and north to Iowa and Wisconsin (Brown, 1983c).

DISTRIBUTION IN LOUISIANA: Central and southeastern ("Florida parishes") areas of the state; absent from the southwestern prairie and the deltaic plain. Rarely collected in the alluvial plain. Occurs in the following drainage basins: Calcasieu River, Lake Pontchartrain, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Ouachita River, Pearl River (black light only), Red River, and Sabine River (Fig. 13.3).

LOUISIANA RECORDS: CATAHOULA P.—Bushley Creek, Bushley Creek (LSUC), Haggerty Creek; DE SOTO P.—Caney Bayou; EAST BATON ROUGE P.—Baton Rouge (3) (LSUC), Beaver Pond Bayou; EAST FELICIANA P.—Redwood Creek, Sandy Creek (2), Sandy Creek (HPB); GRANT P.—4-H Camp Grant Walker (LSUC), Nantachie Creek, Stuart Lake Rec. Area (LSUC); LA SALLE P.—Hemphill Creek; LIVINGSTON P.—Denham Springs (LSUC), Hog Branch; NATCHITOCHES P.—Antoine Creek, Bayou Pierre, Kisatchie Bayou, Santabarb Creek; RAPIDES P.—Castor Creek, Hemphill Creek, Spring Creek; SABINE P.—Lewing Creek; ST. TAMMANY P.—Honey Island Nature Trail (LSUC); TANGIPAHOA P.—Big Creek, Terrys Creek; VERNON P.—Anacoco Bayou (USL), Calcasieu River, Liberty Creek; WEST FELICIANA P.—Alexander Creek, Baker Creek, Bayou Sara, Tunica Bayou, West Fork Thompson Creek; WINN P.—Mill Creek.

HABITAT: Small- to medium-sized streams with sand, gravel, or rarely clay or mud substrates. Most often collected on wood or roots.

Genus *Pelonomus* Erichson, 1847

Pelonomus adults are entirely covered by short erect pubescence including the eyes and antennae. The pectinate antennae do not have the second segments enlarged (Fig. 4.2), and the antennal bases are approximate. The terrestrial larvae were described by Bertrand (1955).

This genus of 12 species is primarily Neotropical in distribution with only one North American representative. *Pelonomus obscurus* LeConte is a riparian or semiaquatic species occurring in swamps and ponds (Brown, 1976).

Pelonomus obscurus LeConte, 1852
Figs. 4.2, 6.4; Map, Fig. 13.4

Pelonomus obscurus LeConte, 1852, *Proc. Acad. Nat. Sci. Phila.* 6:42.

DIAGNOSTIC DESCRIPTION: ADULTS—Reddish to dark brown; entire body, including antennae (Fig. 4.2) and eyes, covered with short, erect pubescence; 4.8-6.5 mm long, 2.0-2.5 mm wide (Fig. 6.4). LARVAE—Not aquatic.

SPECIMENS EXAMINED: 36 adults.

GEOGRAPHIC RANGE: Southeastern United States from South Carolina to Florida, west to Kansas and Texas, and north to southern Illinois and Indiana (Brown, 1983c). There is a single published record from Quebec (LeSage and Harper, 1975).

DISTRIBUTION IN LOUISIANA: Records only from scattered locations in the southern quarter of the state; all probably collected at light (Fig. 13.4). The species was not collected during this study.

LOUISIANA RECORDS: CALCASIEU P.—Sam Houston Jones St. Pk. (LSUC); EAST BATON ROUGE P.—Baton Rouge (4) (LSUC); IBERVILLE P.—St. Gabriel Expt. Sta. (1,2,3) (LSUC); JEFFERSON P.—Grand Isle (LSUC), Grand Isle St. Pk. (LSUC); ST. MARTIN P.—Parks (LSUC).

HABITAT: Since no specimens were collected during this study, habitat details are unknown. See Brown, 1976.

Family Elmidae Shuckard, 1839

Adult Elmidae are typically hard-bodied, having rounded or globular anterior coxae without exposed trochantins, non-retractile legs, 5 tarsal segments and long tarsal claws, and usually slender, 11-segmented antennae. The elongate larvae have retractile gills and opercula bearing internal hooks, and the abdominal sternites or pleurites are not reduced in the anterior 6 segments. Elmids are aquatic in both the adult and larval stages. The common name riffle beetles is applied to the family in the strict sense.

Elmidae is the largest dryopoid family in North America with about 90 described species in 27 genera (Brown, 1983c; Brown, pers. com., Mar. 10 1984). *Dubiraphia, Microcylloepus, Optioservus,* and *Stenelmis* are transcontinental in distribution; *Ancyronyx, Gonielmis, Macronychus, Oulimnius,* and *Promoresia* occur in the East and Southeast. Eighteen other genera are confined to the West; 9 of these are northward extensions of a larger Mexican and Neotropical fauna and are distributed primarily in the Southwest. Six genera, including *Macronychus, Optioservus,* and *Stenelmis,* also occur in the Old World. The above distributions are taken primarily from Brown (1975a, 1981a).

The family has been divided into the subfamilies Larainae and Elminae. The western Larainae consists of 3 species in the genera *Lara* and *Phanocerus.* Adults of this subfamily are riparian, or at most, semi-aquatic. The majority of species belong to the Elminae which are the most completely aquatic of all beetles (Brown, 1987a). Seven of the 25 Nearctic genera in this subfamily occur in Louisiana: *Ancyronyx, Dubiraphia, Gonielmis, Macronychus, Microcylloepus, Optioservus,* and *Stenelmis.*

The elmids have been known by various family names in the past including Elminthidae, Helminthidae, and Helmidae. More than one-half of the Nearctic species were originally described in the genus *Elmis* Latreille (=*Helmis*), now restricted to the Old World. Sanderson (1953, 1954) revised the Nearctic Elmidae in a landmark paper in which he described 7 genera, gave genotype information, and provided keys to the genera of adults and larvae. Brown (1976) discussed the biology, distribution, and taxonomy of the group. In 1978 Brown and White presented aids for the separation of several very similar species. Papers dealing with immature forms are Bertrand (1955, 1965) on the genera, and LeSage and Harper (1976b, 1977) on 5 species.

The taxonomy of the Elmidae will undoubtedly undergo considerable supplementation in the future. Several genera are in need of revision (Brown, 1975b), and many new species are awaiting description. Several genera have larvae which are presently inseparable at the species level.

Genus *Ancyronyx* Erichson, 1847

Ancyronyx is a monotypic genus which occurs only in the eastern and central United States. *Ancyronyx variegata* (Germar) was originally described in the genus *Macronychus.* The larvae were described by Bertrand (1955,

Fig. 13. The known distribution of Dryopidae and Elmidae in Louisiana: 1-4. Dryopidae: 1, *Helichus basalis;* 2, *H. fastigiatus;* 3, *H. lithophilus;* 4, *Pelonomus obscurus.* 5-6. Elmidae: 5, *Ancyronyx variegata;* 6, *Dubiraphia brevipennis.*

1965); adults and larvae were included in Sanderson's (1953) revision of the Elmidae.

Ancyronyx variegata (Germar, 1824)
Figs. 7.1, 11.1; Map, Fig. 13.5

Macronychus variegatus Germar, 1824, *Insectorum Species Novae aut Minus Cognitae, Descriptionibus Illustratae,* p. 89.

DIAGNOSTIC DESCRIPTION: ADULTS—Black with conspicuous yellow or testaceous spots and bands; pronotum smooth with anterior and posterior yellow transverse bands; prosternal process posteriorly nearly as wide as head; elytron smooth with C-shaped vitta anteriorly and elongate subapical spot (Fig. 7.1); hind coxa semiglobular, smaller than other coxae; each tarsal claw with basal tooth; 2.10-2.60 mm long, 0.90-1.10 mm wide. LARVAE—Body robust, brown; prothorax with posterior sternum (so that procoxal cavities are closed posteriorly); abdominal segments 1-8 with posterolateral margins produced into hooked or toothed processes; last abdominal segment not slender and elongate, not spined apically (Fig. 11.1).

COMMENTS: The elytral color pattern is distinctive. When the elytra are encrusted with debris and the pattern is obscured, which is often the case, the species may be recognized by very long, spider-like legs striped black and yellow. The larvae are broad, and unlike other elmids, have lateral abdominal margins that resemble the teeth of a saw.

SPECIMENS EXAMINED: 192 adults, 51 larvae.

GEOGRAPHIC RANGE: Entire eastern North America from Quebec and Ontario to Florida, west to Wisconsin, Kansas, Oklahoma, and Texas (Brown, 1983c).

DISTRIBUTION IN LOUISIANA: North-central, central, west-central, and southeastern ("Florida parishes") areas of the state. Occurs in the following drainage basins: Calcasieu River, Lake Pontchartrain, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Ouachita River, Pearl River, Red River, and Sabine River (Fig. 13.5).

LOUISIANA RECORDS: ALLEN P.—Soapstone Creek, trib. Calcasieu River; BEAUREGARD P.—Bundick Creek (1,2); CALDWELL P.—Castor Creek; CATAHOULA P.—trib. Birds Creek, Bushley Creek (LSUC); EAST BATON ROUGE P.—Beaver Pond Bayou, Comite River (1); EAST FELICIANA P.—Redwood Creek, Sandy Creek (2); GRANT P.—Big Creek, Gray Branch, Nantachie Creek; JACKSON P.—trib. Edwards Branch; LA SALLE P.—Hemphill Creek; LIVINGSTON P.—Hog Branch, Little Natalbany River (HPB), Tickfaw River (HPB,USL), trib. Natalbany River; NATCHITOCHES P.—Santabarb Creek; OUACHITA P.—Guyton Creek; RAPIDES P.—Spring Creek; SABINE P.—Lewing Creek; ST. HELENA P.—Darling Creek, East Hog Branch, Twelvemile Creek; ST. TAMMANY P.—Abita Creek, Bogue Falaya River, East Fork Little Bogue Falaya River, Gum Creek, Mill Creek, Talisheek Creek (2), Tchefuncte River; TANGIPAHOA P.—Big Creek (USL), Chappepeela Creek (1,2), Natalbany River, Selzers Creek, Tangipahoa River, Terrys Creek, creek w of Hammond (HPB); UNION P.—Little Corney Bayou; VERNON P.—Calcasieu River, East Anacoco Creek, Sixmile Creek; WASHINGTON P.—Bogue Chitto River, Bogue Lusa Creek, Hays Creek (USL), Mill Creek, North Carson Creek, Silver Creek; WEBSTER P.—Caney Creek; WEST FELICIANA P.—Baker Creek, Thompson Creek (HPB), West Fork Thompson Creek.

HABITAT: Sandy and/or gravelly streams and rivers of all sizes, rarely in mud- or clay-bottomed streams. Most often collected on wood or roots.

Genus *Dubiraphia* Sanderson, 1954

Pronotum without carinae, each elytron with a longitudinal vitta or 2 maculae, prosternal process posteriorly much narrower than the head, transverse hind coxae, and fringes of tomentum on the anterior tibiae distinguish adult *Dubiraphia* from other genera of elmids in Louisiana. The larvae are easily recognized, having a very long and slender apical abdominal segment with the operculum confined to the posterior third (Fig. 11.2). Larval *Dubiraphia* cannot be identified to species.

Dubiraphia is indigenous to North America and is one of the most widely distributed genera on the continent. Eleven species have been described and several others are awaiting description.

The genus was erected by Sanderson (1954) to include 4 of the species listed in Hinton's (1936) recharacterization of *Simsonia*. Sanderson referred to the original description of *Simsonia* and cited features not applicable to North American species. Hilsenhoff (1973) doubled the size of the genus with the addition of 5 new species, including *D. brevipennis* from Louisiana. This publication provided a key to the species of the central United States and photographs of male genitalia. The genus is badly in need of revision because of numerous undescribed taxa and systematic problems, particularly in the Southeast (Brown, 1975b; Brown, pers. com., June 18 1980). A new species, *D. harleyi*, was recently described from Louisiana (Barr, 1984). A generic description of the larvae of *Dubiraphia* was published by Bertrand in 1955.

Four described and perhaps 3 undescribed species of *Dubiraphia* are known from Louisiana (Barr, 1984; Brown, pers. com., June 18 1980). While some specimens of these "new species" are readily separable from known species, other individuals have characteristics which overlap those of *D. brevipennis* and *D. vittata* Melsheimer. For the purposes of this study, those not keying out in Hilsenhoff (1973) and Barr (1984) are tentatively designated *Dubiraphia* n. spp. A?, B?, and C?. The descriptions and characters given should be considered preliminary at best, as a revision of the genus will likely be necessary to solve the problems involved. For these reasons, laypersons are advised not to attempt species identifications. Dissection of male genitalia is nearly always necessary for identification. The male genitalia of our known species, except *D. parva*?, are illustrated in Figures 10.1-10.3.

Dubiraphia brevipennis Hilsenhoff, 1973
Figs. 7.2, 10.1; Map, Fig. 13.6

Dubiraphia brevipennis Hilsenhoff, 1973, *Ann. Entomol. Soc. Amer.* 66(1):60.

DIAGNOSTIC DESCRIPTION: ADULTS—Palpi and antennae testaceous; elytral length 1.30-1.53 mm; elytron usually vittate, less often bimaculate; vitta or maculae narrow, occupying approximately 3 intervals (from stria 3 to interval 6) at widest point posterior to humerus (Fig. 7.2); femur typically bicolored, darker basally than apically, sometimes entirely dark; tibia and tarsus testaceous; male with penis rather narrow, not more than 1 1/2 times as wide as paramere at midlength, evenly tapered from base to near narrowly rounded tip, length 0.24-0.31 mm; parameres broad, tips broadly rounded and usually wider than at midlength (Fig. 10.1).

COMMENTS: Individuals with bicolored femora are easy to identify. The narrow vittae may resemble those of *D. parva* Hilsenhoff, but *D. brevipennis* has smaller genitalia. When the femora are dark the narrower penis separates this species from *Dubiraphia* n. sp. B?.

SPECIMENS EXAMINED: 154 adults.

GEOGRAPHIC RANGE: Largely unknown; recorded from Louisiana, Alabama, Mississippi, Texas, and Kansas (Brown, pers. com., June 25 1981; Brown, 1983c; Brown and Huggins, 1977; Eiland, 1979).

DISTRIBUTION IN LOUISIANA: Common in the southeast ("Florida parishes"), less common in the west-central and southwestern regions. Occurs in the drainage basins of the Calcasieu River, Lake Pontchartrain, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Pearl River, and Sabine River (Fig. 13.6).

LOUISIANA RECORDS: CALCASIEU P.—Buxton Creek; EAST BATON ROUGE P.—Comite River (1); EAST FELICIANA P.—Amite River, Redwood Creek, Sandy Creek (2); JEFFERSON DAVIS P.—trib. East Bayou Lacassine; LIVINGSTON P.—Hog Branch; SABINE P.—Lewing Creek; ST. HELENA P.—Darling Creek, Tickfaw River; TANGIPAHOA P.—Natalbany River, Tangipahoa River, Terrys Creek, creek w of Hammond (HPB); VERNON P.—Sixmile Creek; WASHINGTON P.—Bogue Chitto River, Mill Creek, Pushepatapa Creek, Silver Creek; WEST FELICIANA P.—West Fork Thompson Creek.

HABITAT: Found most often on roots and aquatic plants occurring in sandy and gravelly streams or occasionally those with a clay substrate.

Dubiraphia harleyi Barr, 1984
Figs. 7.3, 10.2; Map, Fig. 14.1

Dubiraphia harleyi Barr, 1984, *J. Kans. Entomol. Soc.* 57(2):336-339.

DIAGNOSTIC DESCRIPTION: ADULTS—Palpi darker than antennae; basic body color black; large, elytral length 1.67-2.02 mm; elytron with straight, narrow vitta covering 1 I/2 to 2 I/2 intervals (usually stria 3 to interval 6) at widest point posterior to humerus (Fig. 7.3); femur and tibia black with silvery sheen, darker than tarsus; male with penis very long and slender, basal three-fourths tapered evenly to elongated tip, length 0.39-0.45 mm; parameres very narrow, narrowest at midlength and flared at tips, more darkly sclerotized than penis (Fig. 10.2).

COMMENTS: This species is quite distinctive. It is by far the largest *Dubiraphia* in the state, as long as the more northern *D. robusta* Hilsenhoff and almost as long as *D. bivittata* (LeConte). The body is entirely dark dorsally except for 2 very narrow, straight vittae. It keys to *D. robusta* in Hilsenhoff (1973) except for the very different genitalia which are very long and slender and have unique parameres.

SPECIMENS EXAMINED: 159 adults.

GEOGRAPHIC RANGE: Unknown; Louisiana (Barr, 1984).

DISTRIBUTION IN LOUISIANA: Scattered localities in the east-central and southeastern ("Florida parishes") regions. Drainage basins involved are the Atchafalaya River, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Ouachita River, and Pearl River (Fig. 14.1).

LOUISIANA RECORDS: AVOYELLES P.—Coulee des Grues, Cou-

lee des Grues (LSUC); LA SALLE P.—Hemphill Creek; ST. LANDRY P.—Bayou Petite Prairie; WASHINGTON P.—Bonner Creek; WEST FELICIANA P.—West Fork Thompson Creek.

HABITAT: Strikingly different types of stream situations ranging from clear, sandy creeks to large, muddy bayous and agricultural drainage ditches. Collected primarily on tree and aquatic plant roots, sometimes on wood.

Dubiraphia parva Hilsenhoff, 1973 ?
Map, Fig. 14.2

Dubiraphia parva Hilsenhoff, 1973, *Ann. Entomol. Soc. Amer.* 66(1):61.

DIAGNOSTIC DESCRIPTION: ADULTS—Palpi and antennae testaceous; elytral length 1.25-1.40 mm; elytron with narrow vitta or maculae covering 3 or 4 intervals (from intervals 3 to 6 or 3 to 7) at widest point posterior to humerus; femur usually bicolored with basal three-fourths dark and apical fourth light, but may be entirely dark; tibia light, often with dark apex; male with penis usually abruptly narrowed near middle with apical third to half very slender, or less often tapered evenly from base to tip, length 0.31-0.37 mm; parameres narrow, tips narrowly rounded and truncate on inner margins (Figures 7.2 and 7.3).

COMMENTS: We hesitate to report this species since we are far from its reported range and have only a few specimens from a single locality. It is similar to *D. brevipennis,* but the male genitalia are longer and the parameres have narrow tips which are truncate on the inner margins. The shape of the penis was found to be variable as mentioned in the the original description. Individuals with the penis suddenly constricted are distinctive; those with the organ gradually tapered could be mistaken for *D. brevipennis.* Most of our specimens have bicolored femora, unlike Hilsenhoff's type. There is also the possibility that this may be an undescribed species. The genitalia average larger than those of all but *D. harleyi.*

SPECIMENS EXAMINED: 13 adults.

GEOGRAPHIC RANGE: Largely unknown; Oklahoma, Mississippi, and Louisiana (Barr, 1981; Brown, pers. com., June 25 1981; Hilsenhoff, 1973).

DISTRIBUTION IN LOUISIANA: Collection made at a single locality in the north-central part of the state in Catahoula Parish; Ouachita River drainage (Fig. 14.2).

LOUISIANA RECORD: CATAHOULA P.—Bushley Creek.

HABITAT: Shallow sandy stream about 35 ft (56 m) wide, water turbid and reddish in color. Beetles were collected from tree roots.

Dubiraphia vittata (Melsheimer, 1844)
Figs. 7.4, 10.3; Map, Fig. 14.3

Elmis vittatus Melsheimer, 1844, *Proc. Acad. Nat. Sci. Phila.* 2:99.

DIAGNOSTIC DESCRIPTION: ADULTS—Palpi testaceous to rufo-testaceous, usually darker than antennae; elytral length 1.30-1.83 mm; elytron usually vittate, less often bimaculate, vitta or maculae broad and fairly constant in width, generally occupying 5 intervals (from stria 2 to interval 7) at widest point posterior to humerus (Fig. 7.4); femur and tibia darker than tarsus, joint may be light; male with penis stout and convex, at least 2 times width of paramere at midlength, distinctly narrowed in apical fourth, length 0.24-0.31 mm; parameres broad, tips broadly rounded (Fig. 10.3).

COMMENTS: The wide vittae and broad penis distinguish this species. The species may be inseparable from

Dubiraphia n. sp. A? unless the genitalia are examined.

SPECIMENS EXAMINED: 198 adults.

GEOGRAPHIC RANGE: Widespread in the East and Midwest from Quebec and Ontario to Florida and possibly as far west as Idaho, Utah, and Arizona (Brown, 1983c; Brown, pers. com., Mar. 10 1984). Records from Louisiana may be the most southern for the species.

DISTRIBUTION IN LOUISIANA: Common in the central, west-central, southeastern ("Florida parishes") areas; scattered localities in the northwestern and north-central parts of the state. Collected in the following drainage basins: Calcasieu River, Lake Pontchartrain, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Ouachita River, Pearl River, Red River, and Sabine River (Fig. 14.3).

LOUISIANA RECORDS: BEAUREGARD P.—Bundick Creek (2), Hickory Branch, Johns Gully; CADDO P.—Cypress Bayou; EAST BATON ROUGE P.—Beaver Bayou, Comite River (1); EAST FELICIANA P.—Foster Creek, Woodland Creek; LA SALLE P.—Trout Creek; LIVINGSTON P.—Spillers Creek, trib. Natalbany River, West Colyell Creek; RAPIDES P.—Spring Creek; SABINE P.—Bayou Scie; ST. HELENA P.—East Hog Branch, Twelvemile Creek; ST. TAMMANY P.—Abita Creek, Bogue Falaya River, Gum Creek, Mill Creek, Talisheek Creek (2); TANGIPAHOA P.—Hamilton Creek (LSUC), Natalbany River; VERNON P.—Liberty Creek, Sixmile Creek; WASHINGTON P.—Bonner Creek, North Carson Creek, Pushepatapa Creek, Silver Creek.

HABITAT: Collected on tree and aquatic plant roots in all kinds of streams, but the majority of these had sand substrates.

Dubiraphia new species A ?
Map, Fig. 14.4

DIAGNOSTIC DESCRIPTION: ADULTS—Palpi testaceous; elytral length 1.38-1.55 mm; elytron with wide vitta covering about 4 intervals (from stria 2 to 5 or 2 to 6) at widest point posterior to humerus; femur and tibia darker than tarsus; male with penis rather narrow, 1 1/2 to 2 times width of paramere at midlength, nearly parallel-sided to short, pointed tip, length 0.25-0.26 mm; parameres broad, tips broadly rounded and flared.

COMMENTS: This species strongly resembles *D. vittata,* but may be separated on the basis of its much narrower penis. Also, the palpi are testaceous whereas those of *D. vittata* are usually darker.

SPECIMENS EXAMINED: 43 adults.

GEOGRAPHIC RANGE: Unknown; Louisiana (Barr, 1981).

DISTRIBUTION IN LOUISIANA: Collected from only a few scattered streams in the northwestern, central, and southeastern ("Florida parishes") areas; Calcasieu River, Lake Pontchartrain, Mermentau-Vermilion-Teche Rivers, and Red River drainage basins (Fig. 14.4).

LOUISIANA RECORDS: CADDO P.—Cypress Bayou; EAST FELICIANA P.—Redwood Creek; EVANGELINE P.—Bayou Nezpique (1); LIVINGSTON P.—West Colyell Creek; TANGIPAHOA P.—Chappepeela Creek (2); VERNON P.—Sixmile Creek; WASHINGTON P.—Mill Creek.

HABITAT: Occurs in different types of watercourses, including those with sand, mud, or clay substrates and with current velocities ranging from none to swift. Inhabits tree roots and aquatic plants.

Fig. 14. The known distribution of Elmidae in Louisiana: 1, *Dubiraphia harleyi;* 2, *D. parva*?; 3, *D. vittata;* 4, *Dubiraphia* n. sp. A?; 5, *Dubiraphia* n. sp. B?; 6, *Dubiraphia* n. sp. C?.

Dubiraphia new species B ?
Map, Fig. 14.5

DIAGNOSTIC DESCRIPTION: ADULTS—Color of palpi variable, ranging from lighter than antennae to slightly darker; elytral length 1.33-1.57 mm; elytron usually vittate, sometimes maculate, vitta or maculae very narrow, 1 to 3 intervals (intervals 3 or 4 to 5 or 6) at widest point posterior to humerus, often faint posteriorly; femur and tibia with bronze sheen, darker than tarsus; male with penis broad, 2 to 2 1/2 times width of paramere at midlength, tip short and bluntly rounded, length 0.25-0.31 mm; parameres wide with broadly rounded, flared tips.

COMMENTS: The broad penis separates this species from *D. brevipennis* and *D. parva,* which also have narrow vittae. The genitalia are similar to those of *D. vittata.*

SPECIMENS EXAMINED: 206 adults.

GEOGRAPHIC RANGE: Unknown; Louisiana (Barr, 1981).

DISTRIBUTION IN LOUISIANA: Occurs in the north-central, southwestern, south-central, and southeastern ("Florida parishes") areas of the state in the drainages of the Atchafalaya River, Calcasieu River, Lake Pontchartrain, Mermentau-Vermilion-Teche Rivers, Ouachita River, and Pearl River (Fig. 14.5).

LOUISIANA RECORDS: ACADIA P.—Bayou Plaquemine Brule, Long Point Gully; ALLEN P.—Bayou Blue; CALCASIEU P.—Indian Bayou; EVANGELINE P.—Bayou Grand Louis, Bayou Nezpique (1,2); JEFFERSON DAVIS P.—trib. East Bayou Lacassine; LIVINGSTON P.—Hog Branch; MOREHOUSE P.—Chemin-a-Haut Bayou (2); POINTE COUPEE P.—Bayou Latenache Drainage Canal; ST. HELENA P.—Darling Creek (LSUC); ST. LANDRY P.—Bayou Mallet; ST. TAMMANY P.—Talisheek Creek (2); UNION P.—Meridian Creek; WASHINGTON P.—Hays Creek.

HABITAT: Most specimens were found on roots, many on waterlogged wood. Although all types of streams were represented, mud and clay substrates constituted the majority.

Dubiraphia new species C ?
Map, Fig. 14.6

DIAGNOSTIC DESCRIPTION: ADULTS—Palpi usually testaceous, rarely darker than antennae; small, elytral length 1.04-1.28 mm; elytron usually bimaculate, sometimes vittate, vitta or maculae narrow and straight, covering about 2 intervals (from stria 3 to interval 5) at widest point posterior to humerus; femur testaceous to golden brown and only slightly darker than tibia and tarsus (hind leg is darkest); male with penis 1 1/2 to 2 1/2 times width of paramere at midlength, sides evenly narrowed to rounded tip, length 0.22-0.28 mm; parameres broad and rounded at tips.

COMMENTS: Most individuals are distinctly smaller than those of other species of *Dubiraphia,* but the largest specimens (females) may be confused with *D. brevipennis.*

SPECIMENS EXAMINED: 80 adults.

GEOGRAPHIC RANGE: Unknown; Louisiana (Barr, 1981).

DISTRIBUTION IN LOUISIANA: Records from scattered localities in the east-central, central, west-central, and southeastern ("Florida parishes") parts of the state, nearly all of which are in different drainage basins. These are the Calcasieu River, Lake Pontchartrain, Mermentau-Vermilion-Teche Rivers,

Ouachita River, Red River, and Sabine River drainages (Fig. 14.6).

LOUISIANA RECORDS: BEAUREGARD P.—Bundick Creek (2); CATAHOULA P.—Bushley Creek; EAST BATON ROUGE P.—Beaver Pond Bayou; NATCHITOCHES P.—Santabarb Creek; RAPIDES P.—Spring Creek; VERNON P.—East Anacoco Creek, Sixmile Creek.

HABITAT: Nearly all specimens were collected in small- and medium-sized streams with sand and gravel substrates. Preferred microhabitats are aquatic moss and tree roots.

Genus *Gonielmis* Sanderson, 1954

Gonielmis is a monotypic genus occurring only in the southeastern United States. Diagnostic characters are provided in the species description of *G. dietrichi* which follows. This species was described as *Helmis dietrichi* by Musgrave (1933) and was later referred to as *Simsonia dietrichi* by Hinton (1936) and by Young (1954). The genus *Gonielmis* was erected for this species by Sanderson in 1954, who indicated that *Simsonia* should be restricted to Australian species. Bertrand (1955) described the larvae.

Gonielmis dietrichi (Musgrave, 1933)
Figs. 7.5, 11.3; Map, Fig. 15.1

Helmis dietrichi Musgrave, 1933, *Proc. Entomol. Soc. Wash.* 35(4):54.

DIAGNOSTIC DESCRIPTION: ADULTS—Body elongate and spindle-shaped, black; pronotum and elytra without carinae; elytron with 2 oblique, elongate yellow or testaceous spots (Fig. 7.5); prosternal process posteriorly much narrower than width of head; hind coxa transverse and same size or larger than other coxae; lateral margin of fourth abdominal sternite with lobe bent upward to clasp epipleuron; leg dark with yellow tibia; anterior tibia with medial fringe of tomentum; 2.0-2.6 mm long, 0.95-1.10 mm wide. LARVAE—Brown; prothorax without posterior sternum; mesopleuron divided into 2 parts; abdominal segments 1-7 with pleura, humped dorsally and bearing conspicuous scale-like hairs; last abdominal segment slightly emarginate at apex, not spined (Fig. 11.3).

COMMENTS: Oblique elytral maculae are unique among Louisiana elmids, and the distinctive spindle-shaped body is recognizable even in encrusted specimens. The larvae are distinguished by dorsal abdominal humps which are most prominent posteriorly.

SPECIMENS EXAMINED: 52 adults, 240 larvae.

GEOGRAPHIC RANGE: The Atlantic and East Gulf Coastal Plain provinces only; South Carolina, Georgia, Florida, Alabama, Mississippi, and Louisiana (Barr, 1981; Brown, 1983c). Sinclair's (1964) Tennessee record was in error (Brown and White, 1978). Louisiana records are the most western for the species.

DISTRIBUTION IN LOUISIANA: Collected only in the southeastern part of the state in Washington and St. Tammany parishes from the Pearl River and Lake Pontchartrain drainage basins (Fig. 15.1).

LOUISIANA RECORDS: ST. TAMMANY P.—Bogue Falaya River; WASHINGTON P.—Bogue Lusa Creek, Bonner Creek, Crains Creek, Foster Creek, Muster Ground Creek, Pushepatapa Creek, Silver Creek.

HABITAT: Collected only from small- to medium-sized, acidic, spring-fed streams with sand and/or gravel substrates. Usually found on roots or aquatic moss, less often on wood or plants.

Genus *Macronychus* Müller, 1806

Adults of this genus have short, 7-segmented antennae with the apical segments enlarged (Fig. 4.3), a pronotum with 2 basal sublateral carinae, each elytron with one sublateral carina, the prosternal process posteriorly nearly as wide as head, and the hind coxae semiglobular and smaller than other coxae. The larvae have open procoxal cavities, divided mesopleural sclerites, and pleura on abdominal segments 1-6 only.

One species, *Macronychus glabratus* Say, occurs in eastern North America; Old World species include 2 from the Orient and one from Europe. Hinton redescribed *Macronychus* and described a new species in a 1940 synopsis. The genus was reviewed by Sanderson (1954) in his revision of Nearctic elmid genera. A description of the larvae of *Macronychus* was published by Bertrand (1955); the larvae and pupae of *M. glabratus* were described by LeSage and Harper (1976b, 1977). Various aspects of the life cycle and behavior of this species have been detailed by West (1929a), Davis and Finni (1974), and LeSage and Harper (1976a).

Macronychus glabratus Say, 1825
Figs. 4.3, 7.6, 11.4; Map, Fig. 15.2

Macronychus glabratus Say, 1825, *J. Acad. Nat. Sci. Phila.* 5:187.

DIAGNOSTIC DESCRIPTION: ADULTS—Dark brown to black, shining; sublateral elytral carina bordering a conspicuous silvery or golden lateral band of tomentum; 2.50-3.50 mm long, 1.00-1.30 mm wide (Fig. 7.6). LARVAE—Dark brown; prothorax without posterior sternum; mesopleuron divided into 2 parts; abdominal segments 1-6 with pleura and without lateral processes or dorsal humps, posterior margin of each segment with fringe of long hairs; last abdominal segment bearing 2 long, narrowly separated apical spines (Fig. 11.4).

COMMENTS: The species is characterized by a shiny dark brown to black body with broad lateral stripes of silver or gold. The very short antennae are unique and permit easy identification of encrusted individuals. Larvae most closely resemble those of *Stenelmis* and *Microcylloepus*, but both of these have a post-sternum.

SPECIMENS EXAMINED: 576 adults, 91 larvae.

GEOGRAPHIC RANGE: Entire eastern North America from Quebec and Ontario to Florida, west to North Dakota, Kansas, Oklahoma, and Texas (Brown, 1983c).

DISTRIBUTION IN LOUISIANA: North-central, central, west-central, and southeastern ("Florida parishes") areas of the state. Occurs in the following drainage basins: Calcasieu River, Lake Pontchartrain, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Ouachita River, Pearl River, Red River, and Sabine River (Fig. 15.2).

LOUISIANA RECORDS: ALLEN P.—Bundicks Creek (USL), Calcasieu River; BEAUREGARD P.—Bundick Creek (1,2), Bundicks Lake (USL), Johns Gully, Whisky Chitto Creek (USL); BIENVILLE P.—Cypress Creek, Sixmile Creek, SE Arcadia (HPB); CATAHOULA P.—Bushley Creek, Bushley Creek (LSUC), trib. Birds Creek; EAST BATON ROUGE P.—Baton Rouge (1) (LSUC), Beaver Pond Bayou, Comite River (1,2); EAST FELICIANA P.—Amite River, Redwood Creek, Sandy Creek (1,2), Woodland Creek; GRANT P.—Big Creek, Big Creek (HPB), Gray Branch, Nantachie Creek; LA SALLE P.—Doyle Branch, Hemphill Creek; LIVINGSTON P.—Hog Branch, Hog Branch

(LSUC), Little Colyell Creek, Tickfaw River (HPB), Tickfaw River (USL); NATCHITOCHES P.—Bayou Pierre, Kisatchie Bayou, Santabarb Creek; RAPIDES P.—Castor Creek, Hemphill Creek, Spring Creek; RED RIVER P.—trib. Black Lake Bayou; SABINE P.—Lewing Creek; ST. HELENA P.—Darling Creek, East Hog Branch, Tickfaw River, Twelvemile Creek; ST. TAMMANY P.—Abita Creek, Bogue Falaya River, East Fork Little Bogue Falaya River, Tchefuncte River; TANGIPAHOA P.—Big Creek, Big Creek (USL), Chappepeela Creek (1), Natalbany River, Tangipahoa River, Tangipahoa River (USL), Terrys Creek, creek w of Hammond (HPB); VERNON P.—East Anacoco Creek, Liberty Creek, Sixmile Creek; WASHINGTON P.—Bogue Chitto River, Bogue Lusa Creek, Bonner Creek, Crains Creek, Hays Creek, Hays Creek (USL), Lawrence Creek, Muster Ground Creek, Pushepatapa Creek, Silver Creek, Tchefuncte River (USL); WEBSTER P.—Caney Creek; WEST FELICIANA P.—Baker Creek, Bayou Sara, Thompson Creek, Thompson Creek (HPB), Tunica Bayou, West Fork Thompson Creek; WINN P.—Mill Creek.

HABITAT: Sandy and/or gravelly streams and rivers of all sizes, rarely in mud- or clay-bottomed streams. Most often collected on wood, but may be present in a variety of microhabitats.

Genus *Microcylloepus* Hinton, 1935

Adults of this genus are characterized by a pronotum with a transverse sulcus anterior to the middle, a median longitudinal depression, 2 posterior oblique grooves, and 2 sublateral carinae (Fig. 7.7); the prosternal process posteriorly much narrower than width of head; the hind coxae transverse; and the anterior tibiae with medial fringes of tomentum. The larvae have closed procoxal cavities and a narrow mid-dorsal stripe which is enlarged into spots at the posterior margins of the sclerites.

Microcylloepus is primarily Neotropical, with only 4 of the 25 described species occurring in North America. *Microcylloepus pusillus* (LeConte) is transcontinentally distributed and is possibly a species complex (Brown, 1975b). The remaining 3 species are restricted to hot springs in the West.

Hinton erected and described this genus (1935b) and enumerated adult and larval characters to separate *Microcylloepus* from closely related *Heterelmis* (1939a). Differences between these genera were also discussed by Sanderson (1953). Musgrave (1933) gave subspecific status to 4 eastern geographical variants of *M. pusillus*. These 4, plus one western subspecies, were recognized by Brown (1976). Specimens keying to 3 subspecies have been collected in Louisiana.

Microcylloepus pusillus (LeConte, 1852)

Figs. 7.7, 11.5; Map, Fig. 15.3

Stenelmis pusilla LeConte, 1852, *Proc. Acad. Nat. Sci. Phila.* 6:44.

DIAGNOSTIC DESCRIPTION: ADULTS—Brown to black, body carinate and deeply punctate; elytron unmarked, with one longitudinal vitta, or bimaculate; 1.65-2.20 mm long, 0.68-0.90 mm wide (Fig. 7.7). LARVAE—Dark brown to black with narrow white mid-dorsal stripe enlarged into spot at posterior margin of each sclerite, usually also with narrow sublateral stripes; prothorax with posterior sternum; posterolateral margins of abdominal segments without processes; last abdominal segment without apical spines (Fig. 11.5).

COMMENTS: Easily identified, *M. pusillus* is very carinate and punctate

dorsally, while species of a similar size (*G. dietrichi*, *Optioservus trivittatus* (Brown), *Dubiraphia* spp.) are smooth dorsally. Specimens keying to the subspecies *M. p. pusillus* (LeConte) (elytra quadrimaculate), *M. p. aptus* (Musgrave) (elytra bivittate), and *M. p. loedingi* (Musgrave) (elytra immaculate) have been collected in the state. *Microcylloepus p. aptus* is reported here outside of the published range (Brown, 1983c). Problems arose with subspecific designations so we have chosen to report our collections at the species level. A series of specimens exhibiting a range of elytral characters from vittate to maculate were collected at one locality; marked and unmarked individuals were collected together at another site. Specimens from 6 sites could not be confidently assigned to a subspecies. These appeared to be intermediate between *M. p. aptus* and *M. p. pusillus* with the vittae complete medially and interrupted laterally. Quadrimaculate individuals were most numerous in the collections; immaculate ones were the least common and were taken only in the "Florida parishes." Larval *M. pusillus* superficially resemble small *Stenelmis* larvae, but the latter never have a series of white spots located on the mid-dorsal stripe.

SPECIMENS EXAMINED: 232 adults, 154 larvae.

GEOGRAPHIC RANGE: Quebec and the entire United States from Maine to Florida, west to Oregon, California, and Mexico. The eastern subspecies: *M. p. pusillus* from Maine to Florida and west to California, *M. p. aptus* from Virginia to northern Florida, *M. p. loedingi* in the Atlantic and Gulf coastal plains, and *M. p. perditus* (Musgrave) from Florida (Brown, 1983c; Morse et al., 1980).

DISTRIBUTION IN LOUISIANA: North-central, east-central, west-central, central, and southeastern ("Florida parishes") areas of the state. Occurs in the following drainage basins: Calcasieu River, Lake Pontchartrain, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Ouachita River, Pearl River, Red River, and Sabine River (Fig. 15.3).

LOUISIANA RECORDS: BEAUREGARD P.—Bundick Creek (2); CATAHOULA P.—Bushley Creek (LSUC), trib. Birds Creek; EAST BATON ROUGE P.—Beaver Pond Bayou (LSUC), Comite River (1); EAST FELICIANA P.—Amite River; GRANT P.—Big Creek, Gray Branch; JACKSON P.—trib. Edwards Branch; LA SALLE P.—Doyle Branch, Hemphill Creek; LIVINGSTON P.—Hog Branch; NATCHITOCHES P.—Bayou Pierre; OUACHITA P.—Guyton Creek; RAPIDES P.—Spring Creek; SABINE P.—Lewing Creek; ST. HELENA P.—East Hog Branch, Tickfaw River; ST. TAMMANY P.—Abita Creek, Bogue Falaya River, East Fork Little Bogue Falaya River, Gum Creek, Talisheek Creek (2); TANGIPAHOA P.—Tangipahoa River, Terrys Creek, creek w of Hammond (HPB); UNION P.—Little Corney Bayou, Meridian Creek; VERNON P.—East Anacoco Creek, Sixmile Creek; WASHINGTON P.—Bogue Chitto River, Bogue Lusa Creek, Foster Creek, Hays Creek, Mill Creek, Muster Ground Creek, Pushepatapa Creek, Silver Creek; WEST FELICIANA P.—Bayou Sara, West Fork Thompson Creek.

HABITAT: Sandy and/or gravelly streams and rivers of all sizes, rarely in clay-bottomed streams. Most often collected on roots and aquatic moss.

Genus *Optioservus* Sanderson, 1954

Optioservus adults may be distinguished from those of other Louisiana

Fig. 15. The known distribution of Elmidae in Louisiana: 1, *Gonielmis dietrichi;* 2, *Macronychus glabratus;* 3, *Microcylloepus pusillus;* 4, *Optioservus trivittatus;* 5, *Stenelmis antennalis;* 6, *S. bicarinata.*

genera by their plump, robust form, very short basal sublateral pronotal carinae, lack of elytral carinae, transverse hind coxae, and each anterior tibia with a medial fringe of tomentum. The dark brown larvae are triangular in cross-section and have a laterally expanded, hood-like pronotum, open procoxal cavities, and undivided mesopleural sclerites. Larval *Optioservus* cannot be identified to species.

This genus, with 22 species, is native to North America and Japan. Here it is distributed transcontinentally, but six of the 13 species are primarily eastern. One species, *Optioservus trivittatus* (Brown), occurs in Louisiana.

Sanderson (1954) erected the genus to include species previously in *Elmis, Helmis, Limnius,* and *Heterlimnius.* Due to his untimely death, Collier's (1969) revision of the genus remains unpublished except for descriptions of 2 new species authored by Collier and included in Brown (1976). *Optioservus* was revised again in 1978 by White who described 3 new species and relegated 4 others to synonymy. The larvae were described by Bertrand (1955).

Optioservus trivittatus (Brown, 1930)
Figs. 7.8, 11.6; Map, Fig. 15.4

Limnius trivittatus Brown, 1930, *Canadian Entomol.* 62:91.

DIAGNOSTIC DESCRIPTION: ADULTS—Dark brown; elytron with sutural and medial testaceous vittae; 1.69-2.19 mm long, 0.78-1.14 mm wide (Fig. 7.8). LARVAE—See Fig. 11.6.

COMMENTS: No other elmid in Louisiana has such a plump, rounded body form, or a sutural vitta. Occasional individuals have a lateral vitta on the elytral margin. Larvae of *Optioservus* are similar to those of *M. glabratus* in that they lack a posterior sternum. They differ in having undivided mesopleural sclerites, the body triangular in cross-section, and a hood-like pronotum with expanded lateral margins.

SPECIMENS EXAMINED: 42 adults, 62 larvae.

GEOGRAPHIC RANGE: Eastern North America from Quebec to northern Alabama, west to Wisconsin, Indiana, and Louisiana (Barr, 1981; Eiland, 1979; White, 1978). There is a questionable record from Missouri (Brown, pers. com., Mar. 10 1984). Louisiana records represent a significant southwestward extension of the range for the species given by White.

DISTRIBUTION IN LOUISIANA: Collected only at 2 sites in Washington Parish from the Pearl River drainage basin in the southeastern part of the state (Fig. 15.4).

LOUISIANA RECORDS: WASHINGTON P.—Mill Creek, Muster Ground Creek.

HABITAT: These sites are small streams with sand and gravel substrates and brown-stained, acidic waters. All specimens were collected in gravelly riffles or narrow chutes about one-half meter deep with gravel substrates.

Genus *Stenelmis* Dufour, 1835

Adult *Stenelmis* have the prosternal process narrower posteriorly than the width of the head, have transverse hind coxae, and lack tomentum on the anterior tibiae. In addition to the characters given in the key, the larvae have the propleura undivided, the mesopleura divided, and 2 distinct frontal teeth on the anterior margin of the head (Fig. 11.7).

Stenelmis is the most widely distributed elmid genus with many representatives in Europe, Asia, and Africa. It is the largest genus in North America, with all but one of the 29 described species occurring east of the 100th meri-

dian. Seven described and 2 probably undescribed species occur in Louisiana.

Sanderson (1938) revised the genus in North America, describing 18 new species and reducing 4 to synonymy. Some of the paratypes of *S. grossa* were from Louisiana. His monograph discussed the life history and distribution of the species as well as the morphology and taxonomy. Since 1938 only 4 new species have been described. Revision of the genus is needed due to the presence of several undescribed species (Brown, 1975b). Kurt Schmude at the University of Wisconsin has recently undertaken this study as a Ph.D. dissertation project. Dissection of male genitalia is often necessary to separate the species.

Larval *Stenelmis* cannot be identified to species. Although the larvae of 11 described and 3 undescribed species were characterized by Shepard (1980), the larvae of many species are unknown. Three of the species treated by Shepard occur in Louisiana. The life history, larvae, and pupae of *S. crenata* (Say) were described by LeSage and Harper (1976a, 1976b, 1977).

Stenelmis antennalis Sanderson, 1938
Figs. 8.1, 9.1; Map, Fig. 15.5

Stenelmis antennalis Sanderson, 1938, *Univ. Kansas Sci. Bull.* 25(22):695.

DIAGNOSTIC DESCRIPTION: ADULTS—Body black; antenna bicolored, basal 3-6 segments testaceous, remainder black; elytron distinctly vittate or bimaculate, humeral spot not covering umbone (Fig. 8.1); surface of femur granulate; last tarsal segment distinctly longer than other 4 combined (Fig. 4.6); male with swelling or ridge on inner surface of middle tibia (Fig. 4.5); penis slender and blunt-tipped, lateral processes narrowly elongated (Fig. 9.1); 2.50-2.70 mm long, 1.00 mm wide.

COMMENTS: This species and *S. lateralis* are the smallest members of the genus occurring in the state. The bicolored antennae are diagnostic; the number of testaceous vs. black segments varies. The vittae may be entire or broken, contrary to Sanderson's (1938) description of "always entire."

SPECIMENS EXAMINED: 25 adults.

GEOGRAPHIC RANGE: The Atlantic and Gulf coastal plains from South Carolina to Louisiana (Barr, 1981; Brown, 1983c). Louisiana records represent a westward extension of the known range and include the first from west of the Mississippi River.

DISTRIBUTION IN LOUISIANA: West-central, central, and southeastern ("Florida parishes") areas of the state, occurring in the following drainage basins: Calcasieu River, Lake Pontchartrain, Ouachita River (black light only), Pearl River, and Sabine River (Fig. 15.5).

LOUISIANA RECORDS: BEAUREGARD P.—Bundicks Lake (USL); EAST FELICIANA P.—Amite River; GRANT P.—Stuart Lake Rec. Area (LSUC); ST. HELENA P.—Tickfaw River; ST. TAMMANY P.—Bogue Falaya River; TANGIPAHOA P.—Terrys Creek; VERNON P.—East Anacoco Creek; WASHINGTON P.—Bogue Chitto River, Bogue Lusa Creek, Crains Creek, Muster Ground Creek.

HABITAT: Specimens were collected from sandy and gravelly streams on wood, moss, and roots.

Stenelmis bicarinata LeConte, 1852
Figs. 8.2, 9.2; Map, Fig. 15.6

Stenelmis bicarinatus LeConte, 1852, *Proc. Acad. Nat. Sci. Phila.* 6:44.

DIAGNOSTIC DESCRIPTION: ADULTS—Body medium to dark brown; pronotum indistinctly to dis-

tinctly granulate, tubercles prominent, median sulcus deep with ridged margins; lateral margins of pronotum in dorsal view not strongly divergent in anterior third, either parallel-sided or only slightly divergent; elytron bimaculate, often faintly, humeral spot not covering umbone; elytron with base of third interval moderately elevated, each stria with distinct punctures becoming fainter at posterior third (Fig. 8.2); surface of femur granulate; last tarsal segment distinctly longer than previous 4 combined (Fig. 4.6); male without swelling or ridge on inner surface of middle tibia; penis slender and narrowed apically, lateral processes narrowly elongated (Fig. 9.2); 2.94-3.46 mm long, 1.05-1.32 mm wide.

COMMENTS: Sanderson's (1938) widely followed redescription of *S. bicarinata* was apparently in error, and does not fit LeConte's type (Brown, 1987b). The real *S. bicarinata* keys out to *S. convexula* in Brown (1976) but may be distinguished from it by the following characters: male without ridge on middle tibia; penis with narrow, elongate lateral processes; elytra not very convex, striae and basal elevations of third intervals more distinct; and more prominent pronotal tubercles and sulcus. *Stenelmis bicarinata* is also quite similar in appearance to *S. sinuata* LeConte, but the latter has the lateral margins of the pronotum strongly divergent in the anterior third, and is more strongly sculptured with larger, deeper punctures on the elytra and very prominent pronotal tubercles.

SPECIMENS EXAMINED: 649 adults.

GEOGRAPHIC RANGE: From central Ohio and Indiana south to Florida and west to Oklahoma and Texas (Brown, 1987b). Uncommon except in the southern part of its range (Brown, pers. com., Mar. 10 1984).

DISTRIBUTION IN LOUISIANA: Central, west-central, and southeastern ("Florida parishes") areas of the state. Occurs in the following drainage basins: Calcasieu River, Lake Pontchartrain, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Ouachita River, Pearl River, Red River, and Sabine River (Fig. 15.6).

LOUISIANA RECORDS: ALLEN P.—Calcasieu River, Soapstone Creek; BEAUREGARD P.—Bundick Creek (1,2), near Rosepine (LSUC); CATAHOULA P.—Bushley Creek; EAST BATON ROUGE P.—Baton Rouge (2) (LSUC), Beaver Pond Bayou, 1.2 mi S Central (2) (LSUC); EAST FELICIANA P.—Amite River, Idlewild Expt. Sta. (LSUC), Sandy Creek (2); GRANT P.—Big Creek, Big Creek (HPB), Gray Branch, Nantachie Creek, Stuart Lake Rec. Area (LSUC); JACKSON P.—trib. Edwards Branch; LIVINGSTON P.—Hog Branch, Little Natalbany River (HPB), Tickfaw River (HPB); NATCHITOCHES P.—Antoine Creek, Bayou Pierre, Kisatchie Bayou, Little Bayou Pierre, Malaudos Creek, Santabarb Creek; OUACHITA P.—Guyton Creek; RAPIDES P.—Castor Creek, Hemphill Creek, Spring Creek; RED RIVER P.—trib. Black Lake Bayou; SABINE P.—Bayou Scie, Lewing Creek; ST. HELENA P.—Twelvemile Creek; ST. TAMMANY P.—Abita Creek, East Fork Little Bogue Falaya River, Honey Island Nature Trail (LSUC), I-10 at Pearl River (LSUC), Talisheek Creek (2); TANGIPAHOA P.—Big Creek, Natalbany River, Tangipahoa River, Terrys Creek, creek w of Hammond (HPB); VERNON P.—East Anacoco Creek, Liberty Creek, Sixmile Creek; WASHINGTON P.—Bogue Lusa Creek, Foster Creek, Muster Ground Creek, Pushepatapa Creek, Silver Creek; WEST FELICIANA P.—Bayou Sara.

HABITAT: Streams of all sizes, usually with sand and/or gravel substrates but occasionally clay- or mud-bottomed. Most often collected on wood, gravel, and roots.

Stenelmis convexula Sanderson, 1938
Figs. 8.3, 9.3; Map, Fig. 16.1

Stenelmis convexula Sanderson, 1938, *Univ. Kansas Sci. Bull.* 25(22):704.

DIAGNOSTIC DESCRIPTION: ADULTS—Body medium to dark brown; pronotum indistinctly granulate to smooth, often shiny, tubercles not prominent, median sulcus shallow with rounded margins; lateral margins of pronotum in dorsal view parallel-sided; elytron vittate or bimaculate, often faintly, humeral spot not covering umbone; elytron very smooth and convex, usually with little or no basal elevation of third interval, punctures of striae shallow (Fig. 8.3); surface of femur granulate; last tarsal segment distinctly longer than previous 4 combined (Fig. 4.6); male with swelling or ridge on inner surface of middle tibia (Fig. 4.5); penis slender, lateral processes broadly rounded (Fig. 9.3); 3.09-3.64 mm long, 1.21-1.44 mm wide.

COMMENTS: Unlike *S. bicarinata,* males of this species have a ridge on the middle tibia (contrary to Brown's 1976 key). In addition, the elytra are more convex and smooth, appearing inflated especially between humeri, with shallow striae and little or no basal elevation of the third intervals. The pronotum is also smooth with tubercles indistinct and median sulcus shallow.

SPECIMENS EXAMINED: 119 adults.

GEOGRAPHIC RANGE: The Atlantic and East Gulf coastal plains from South Carolina to Louisiana (Barr, 1981; Brigham, 1982; Brown, pers. com., Mar. 10 1984). Reports of this species in Oklahoma and Texas (e.g., Brown, 1956, 1976; Sanderson and Brown, 1959) concern *S. bicarinata,* with which *S. convexula* has been widely confused. Louisiana records are the most western for the species.

DISTRIBUTION IN LOUISIANA: Collected only in the southeastern ("Florida parishes") part of the state in the Lake Pontchartrain and Pearl River drainage basins (Fig. 16.1).

LOUISIANA RECORDS: ST. HELENA P.—Darling Creek; ST. TAMMANY P.—Bogue Falaya River, East Fork Little Bogue Falaya River, Honey Island Nature Trail (LSUC); TANGIPAHOA P.—Big Creek; WASHINGTON P.—Bogue Lusa Creek, Crains Creek, Mill Creek, Muster Ground Creek, Silver Creek.

HABITAT: Small- and medium-sized sandy streams often with gravelly riffles. Most often collected on wood, gravel, and aquatic plants.

Stenelmis crenata (Say, 1824) ?
Figs. 8.4, 9.4; Map, Fig. 16.2

Elmis crenatus Say, 1824, Appendix Vol. II, Keating's Expedition to Source of St. Peter's River Under Maj. Long, p. 275.

DIAGNOSTIC DESCRIPTION: ADULTS—Body dark brown; in dorsal view lateral margins of pronotum in anterior third slightly rounded and either parallel or angled anteromedially, appearing to clasp head; elytron faintly vittate, bimaculate, or nearly immaculate in Louisiana specimens, humeral spot not covering umbone; elytron with base of third interval strongly elevated (Fig. 8.4); surface of femur granulate; last tarsal segment not distinctly longer than previous 4 combined (Fig. 4.7); male with very indistinct swelling or ridge, perhaps only a few enlarged spines, on inner surface of middle tibia; penis stout and blunt-tipped, lateral

processes broadly rounded (Fig. 9.4); 3.31-3.67 mm long, 1.27-1.47 mm wide.

COMMENTS: There is considerable doubt as to whether Louisiana specimens are *S. crenata* or represent an undescribed species. Material redescribed by Sanderson (1938) as *S. crenata* may not be conspecific with the species Say described from Pennsylvania (Brown, pers. com., Jan. 29 1984, Apr. 19 1984). In addition, there are the following differences between our specimens and Sanderson's redescription: (1) the elytra are significantly longer and do not appear as described, (2) the elytral vittae/maculae are very faint to invisible, (3) the male mesotibial ridges are barely visible. The shape of the pronotum is characteristic and unlike that of other Louisiana species. *Stenelmis crenata*? is more robust than either *S. sinuata* or *S. bicarinata* and is much more granulate than the latter. *Stenelmis lateralis* is our only other species having the last tarsal segment not distinctly longer than the previous 4 combined.

SPECIMENS EXAMINED: 15 adults.

GEOGRAPHIC RANGE: Entire eastern North America from Newfoundland and Quebec to northern Florida, west to Minnesota, Kansas, Oklahoma, and Texas (Brown, 1976, 1983c).

DISTRIBUTION IN LOUISIANA: Collected only in the southeastern ("Florida parishes") part of the state in the Lake Pontchartrain, Lower Mississippi River, and Pearl River drainage basins (Fig. 16.2).

LOUISIANA RECORDS: EAST FELICIANA P.—Hurricane Creek, Woodland Creek; WASHINGTON P.—Hays Creek, Mill Creek, Silver Creek; WEST FELICIANA P.—Bayou Sara, W. Feliciana Parish (LSUC).

HABITAT: Small- and medium-sized streams with sand and gravel substrates, most often on gravel and roots.

Stenelmis grossa Sanderson, 1938
Figs. 8.5, 9.5; Map, Fig. 16.3

Stenelmis grossa Sanderson, 1938, *Univ. Kansas Sci. Bull.* 25(22):686.

DIAGNOSTIC DESCRIPTION: ADULTS—Dark brown to black; shape of lateral pronotal margins very variable; elytron bimaculate, often faintly, humeral spot not covering umbone; elytron with base of third interval strongly elevated (Fig. 8.5); surface of femur punctate; last tarsal segment distinctly longer than previous 4 combined (Fig. 4.6); male with swelling or ridge on inner surface of middle tibia (Fig. 4.5); penis stout, lateral processes subangulate anteriorly (Fig. 9.5); large, 3.25-3.60 mm long, 1.25-1.40 mm wide.

COMMENTS: *Stenelmis grossa* may superficially resemble *S. sinuata,* but it is our only species without granulate femora. This character is best seen when the beetle is dry. The elytra range from faintly quadrimaculate to immaculate, and the shape of the lateral pronotal margins is extremely variable.

SPECIMENS EXAMINED: 937 adults.

GEOGRAPHIC RANGE: The Gulf Coastal Plain only; Alabama, Mississippi, Louisiana, Arkansas, Texas, and Oklahoma (Brown, 1983c; Eiland, 1979).

DISTRIBUTION IN LOUISIANA: Statewide with the exception of the deltaic plain. Rare in the alluvial plains of the Red and Mississippi rivers. Occurs in the following drainage basins: Atchafalaya River, Calcasieu River, Lake Pontchartrain, Lower Mississippi River, Mermentau-Vermilion-Teche Rivers, Ouachita River, Pearl River, Red River, Sabine River, and Terrebonne (Fig. 16.3).

LOUISIANA RECORDS: ACADIA P.—Bayou Plaquemine Brule, Long Point Gully; ALLEN P.—Bayou Blue, Calcasieu River, Mitchell Creek, Soap-

stone Creek, trib. Calcasieu River; AVOYELLES P.— Coulee des Grues (LSUC); BEAUREGARD P.—Bundick Creek (2), Hickory Branch, Johns Gully; BIENVILLE P.—Cypress Creek, Leatherman Creek, Redfield Branch, SE Arcadia (HPB), NE Bienville (HPB); BOSSIER P.—Martin Creek, trib. Little Cypress Bayou; CADDO P.—Cypress Bayou, Flag Branch, Myrtis Mill Creek, Pawpaw Bayou, Shettleworth Bayou; CALCASIEU P.—Buxton Creek; CALDWELL P.—Castor Creek, trib. Flat Creek; CATAHOULA P.—Bushley Creek, Bushley Creek (LSUC), Haggerty Creek, trib. Birds Creek; CLAIBORNE P.—Middle Fork Bayou d'Arbonne; DE SOTO P.—Bull Bayou, Caney Bayou; EAST BATON ROUGE P.—Beaver Bayou, 1.2 mi S Central (1) (LSUC); EAST FELICIANA P.—Amite River, Little Comite Creek (LSUC), Redwood Creek; EVANGELINE P.—Bayou des Cannes, Bayou Cocodrie (USL), Bayou Grand Louis, Bayou Nezpique (1,2); GRANT P.—Gray Branch, Nantachie Creek, Stuart Lake Rec. Area (LSUC); JACKSON P.—trib. Edwards Branch; JEFFERSON DAVIS P.—Bayou Serpent, trib. East Bayou Lacassine; LA SALLE P.—Doyle Branch, Hemphill Creek; LINCOLN P.—trib. Choudrant Creek; LIVINGSTON P.—Blood River, Little Colyell Creek, Spillers Creek, trib. Natalbany River, West Colyell Creek; MOREHOUSE P.—Chemin-a-Haut Bayou (2); NATCHITOCHES P.—Malaudos Creek, Santabarb Creek; OUACHITA P.—Guyton Creek; POINTE COUPEE P.—Bayou Grosse Tete, Bayou Latenache Drainage Canal; RAPIDES P.—Castor Creek, Germany Branch (HPB), Hemphill Creek, Spring Creek; RED RIVER P.—trib. Black Lake Bayou, trib. Brushy Creek; SABINE P.—Bayou Scie; ST. HELENA P.—East Hog Branch; ST. LANDRY P.—Bayou Mallet, Little Wauksha Bayou; ST. TAMMANY P.—Abita Creek, East Bedico Creek, Gum Creek, Honey Island Nature Trail (LSUC), Talisheek Creek (2); TANGIPAHOA P.—Selzers Creek; UNION P.—Bayou de Loutre, Cypress Creek, Little Corney Bayou, Meridian Creek; VERNON P.—Calcasieu River, East Anacoco Creek, Liberty Creek; WASHINGTON P.—Bonner Creek, Foster Creek, Mill Creek, North Carson Creek, Junction La. 16 & 60 (USL); WEBSTER P.—Caney Creek, Holder Creek, Indian Creek; WEST BATON ROUGE P.—Bayou Poydras; WEST FELICIANA P.—Alexander Creek, West Fork Thompson Creek; WINN P.—E trib. Kiesche Creek, Mill Creek.

HABITAT: Found in all types of streams and rivers, occurs most often on gravel, wood, or roots.

Stenelmis lateralis Sanderson, 1938
Figs. 8.6, 9.6; Map, Fig. 16.4

Stenelmis lateralis Sanderson, 1938, *Univ. Kansas Sci. Bull.* 25(22):672.

DIAGNOSTIC DESCRIPTION: ADULTS—Dark brown to black; elytron distinctly vittate, vitta broad, covering umbone and widened in apical third, extending from stria 1 to interval 6 (Fig. 8.6); surface of femur granulate; apical tarsal segment not distinctly longer than previous 4 combined (Fig. 4.7); male with swelling or ridge on inner surface of middle tibia (Fig. 4.5); penis narrowed medially and blunt-tipped, lateral processes absent (Fig. 9.6); 2.65-3.00 mm long, 0.95-1.10 mm wide.

COMMENTS: Unmistakable due to its small size and broad elytral vittae which cover most of the elytral space and extend laterad at the umbones and near the apices. The last tarsal segment is not distinctly longer than the previous 4 combined, a character that it shares

Fig. 16. The known distribution of Elmidae in Louisiana: 1, *Stenelmis convexula;* 2, *S. crenata*?; 3, *S. grossa;* 4, *S. lateralis;* 5, *S. sinuata;* 6, *Stenelmis* n. sp.

with *S. crenata*?. Like *Stenelmis* n. sp., this species has no lateral processes on the penis.

SPECIMENS EXAMINED: 9 adults.

GEOGRAPHIC RANGE: Scattered locations in the eastern and midwestern United States; recorded from Pennsylvania, Virginia, South Carolina, Tennessee, Missouri, Kansas, Oklahoma, Arkansas, Louisiana, Mississippi, and Alabama (Barr, 1981; Brown, 1976, 1983c; Eiland, 1979; Huggins et al., 1976; Morse et al., 1980). Louisiana records may be the most southern for the species.

DISTRIBUTION IN LOUISIANA: Collected only at 3 locations in the southeastern ("Florida parishes") part of the state in the Lake Pontchartrain and Pearl River drainage basins (Fig. 16.4).

LOUISIANA RECORDS: EAST BATON ROUGE P.—1.2 mi S Central (2) (LSUC); EAST FELICIANA P.—Idlewild Expt. Sta. (LSUC); WASHINGTON P.—Mill Creek.

HABITAT: The Washington Parish site is a small stream with a sand and gravel substrate and brown-stained, acidic waters. The beetles were collected in gravel riffles.

Stenelmis sinuata LeConte, 1852
Figs. 8.7, 9.7; Map, Fig. 16.5

Stenelmis sinuatus LeConte, 1852, *Proc. Acad. Nat. Sci. Phila.* 6:44.

DIAGNOSTIC DESCRIPTION: ADULTS—Dark brown to black; pronotum distinctly granulate and with prominent tubercles, basal tubercles carinate; lateral margins of pronotum crenate and strongly divergent in anterior third; elytron usually bimaculate, often faintly, humeral spot not covering umbone; elytron with base of third interval strongly elevated, each stria with large, deep punctures (Fig. 8.7); surface of femur granulate; last tarsal segment only slightly longer than previous 4 combined; male without swelling or ridge on inner surface of middle tibia; penis slender and blunt-tipped, lateral processes narrowly rounded (Fig. 9.7); 3.20-3.45 mm long, 1.20-1.35 mm wide.

COMMENTS: This species differs from *S. crenata*? in having the last tarsal segment slightly longer than the previous 4 combined and by having the pronotum flared outward in the anterior third. The degree of pronotal flaring and lateral sinuation varies among individuals. *Stenelmis bicarinata* does not exhibit this pronotal character, and in addition, larger pronotal granulations and deeper elytral punctures cause *S. sinuata* to appear much more sculptured. Most specimens exhibit faint maculae, but a few are unmarked. Louisiana males have no mesotibial ridges. Sanderson (1938) concluded, probably from the lack of such ridges, that all of the 11 specimens he examined were females. Brown (pers. com., Feb. 25 1981, Jan. 29 1984) believes that this species may ultimately be split on the basis of genitalic differences. It appears that all of our specimens are of the same type.

SPECIMENS EXAMINED: 76 adults.

GEOGRAPHIC RANGE: The Atlantic and East Gulf coastal plains of the southeastern United States from South Carolina to Louisiana (Brown, 1983c). Louisiana records are the most western for the species.

DISTRIBUTION IN LOUISIANA: Collected only in the southeastern part of the state in St. Tammany and Washington parishes from the Pearl River and adjacent Lake Pontchartrain drainage basins (Fig. 16.5).

LOUISIANA RECORDS: ST. TAMMANY P.—Gum Creek, Talisheek

Creek (1,2); WASHINGTON P.—Bonner Creek, Foster Creek, Mill Creek, North Carson Creek, Pushepatapa Creek, Silver Creek.

HABITAT: Small- and medium-sized streams with sand and/or gravel substrates. Present in a variety of microhabitats, but most often on gravel, roots, and wood.

Stenelmis new species near *decorata* Sanderson, 1938
Figs. 8.8, 9.8; Map, Fig. 16.6

DIAGNOSTIC DESCRIPTION: ADULTS—Dark brown; pronotum nearly equal in width at base and apex; elytron vittate, bimaculate, or nearly immaculate, humeral spot not covering umbone (Fig. 8.8); surface of femur granulate; last tarsal segment longer than previous 4 combined (Fig. 4.6); male with swelling or ridge on inner surface of middle tibia (Fig. 4.5); penis slender and blunt-tipped, lateral processes absent (Fig. 9.8); 2.50-2.80 mm long, 0.90-1.00 mm wide.

COMMENTS: Description of this species is pending. It is most closely related to *S. decorata,* a more northern and eastern species, which also lacks lateral processes on the penis. Unlike that species, the elytral vittae are not always entire. The new species is also considerably smaller. The genitalia are similar to those of *S. lateralis,* which also lacks lateral processes, but *S. lateralis* has much broader elytral vittae.

SPECIMENS EXAMINED: 120 adults.

GEOGRAPHIC RANGE: Alabama to Texas (Brown, pers. com., May 30 1980).

DISTRIBUTION IN LOUISIANA: North-central, central, and southeastern ("Florida parishes") parts of the state. Collected at only a few localities in the Lake Pontchartrain, Ouachita River, Pearl River, and Mermentau-Vermilion-Teche Rivers drainage basins (Fig. 16.6).

LOUISIANA RECORDS: ACADIA P.—Long Point Gully; EAST BATON ROUGE P.—1.2 mi S Central (2) (LSUC); EVANGELINE P.—Bayou des Cannes; GRANT P.—Stuart Lake Rec. Area (LSUC); JEFFERSON DAVIS P.—trib. East Bayou Lacassine; LIVINGSTON P.—Denham Springs (LSUC); MOREHOUSE P.—Chemin-a-Haut St. Pk. (LSUC); ST. TAMMANY P.—Honey Island Nature Trail (LSUC).

HABITAT: Clay- or mud-bottomed streams and rivers, on wood or gravel.

Distributional Patterns of Species

Geographical Distribution

General.—The dryopoid fauna of Louisiana consists mainly of eastern and coastal plain species. Eastern species are defined as those occurring primarily east of the 100th meridian (from North Dakota to Texas), while coastal plain species occur in the coastal plain from New Jersey southwest to Texas (Bick, 1957). Although several western species occur in Texas, none has been collected in Louisiana. Eleven of the 25 dryopoids occurring in the state are eastern species: *Ectopria thoracica, Helichus basalis, H. fastigiatus, H. lithophilus, Pelonomus obscurus, Ancyronyx variegata, Macronychus glabratus, Optioservus trivittatus, Stenelmis bicarinata, S. crenata*?, and *S. lateralis.* The records of *O. trivittatus* from the "Florida parishes" represent a significant range extension for the species to the southwest. White (1978) reported it from as far south as eastern Tennessee; however, there are recent unpublished records of the species from northern Alabama (Eiland, 1979) and southern Mississippi (Stark, pers. com.,

Jan. 9 1981). Localities for *H. basalis* and *S. lateralis* in the "Florida parishes" are possibly the most southern records. Six dryopoids are coastal plain species: *G. dietrichi, S. antennalis, S. convexula, S. grossa, S. sinuata,* and *Stenelmis* n. sp. The *G. dietrichi, S. antennalis, S. convexula,* and *S. sinuata* records are westward range extensions. Six species were collected only east of the Mississippi River: *G. dietrichi, O. trivittatus, S. convexula, S. crenata?, S. lateralis,* and *S. sinuata. Dubiraphia parva* was the only species collected exclusively west of the river. The records of *S. antennalis* from Beauregard, Grant, and Vernon parishes are the first reports of this species west of the river. *Dubiraphia vittata* and *M. pusillus* are nearly transcontinental in distribution. The complete ranges of *D. brevipennis, D. harleyi, D. parva?,* and *Dubiraphia* n. spp.? are not known.

Of the 191 sites sampled, 138 were productive (i.e., dryopoids were collected). The 53 unproductive sites are scattered throughout the state, but certain patterns were observed and will be discussed in the following section on physiography and vegetation.

Species were not uniformly distributed in the state; while some areas were rich in species, others appeared to be entirely devoid of dryopoids. Some species were widespread and common almost everywhere; others had very localized distributions or were infrequently collected at scattered localities. The commonness of each species in the state was calculated as a percentage of the total number of productive collections (N = 142), illustrated

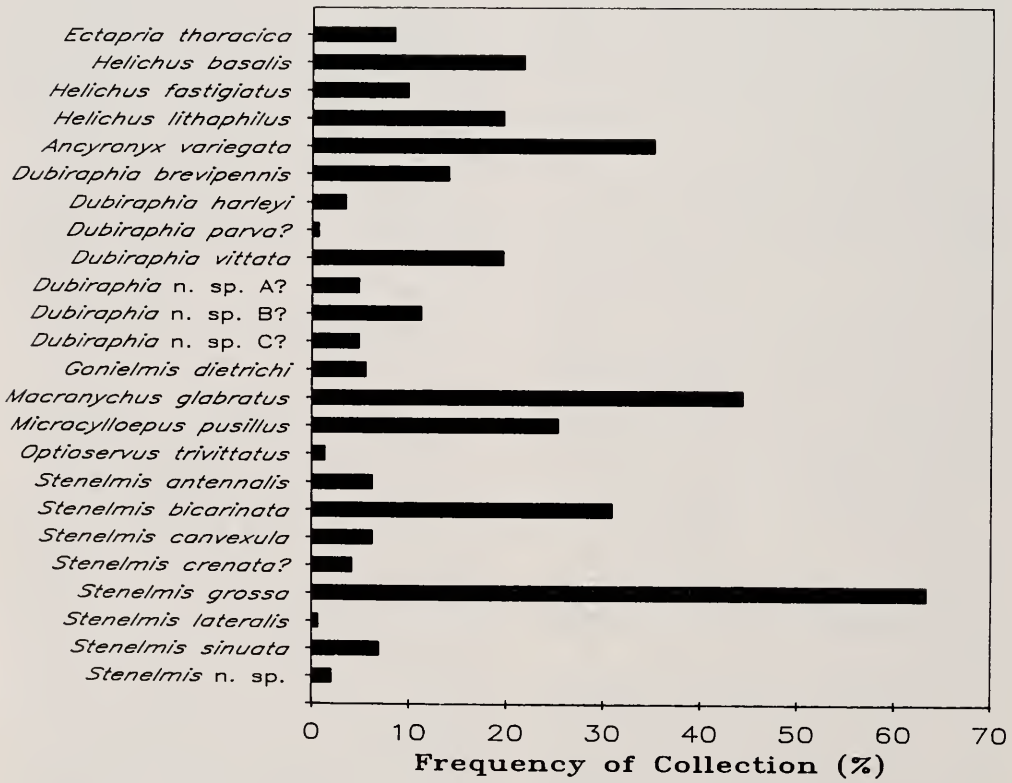

Fig. 17. Commonness of dryopoid species in Louisiana based on frequency of collection (N = 142).

in Figure 17. Productive collections exceeded productive sites (138) due to multiple collections at 3 sites (see Materials and Methods, Selection of Sites). *Stenelmis grossa* was the most frequently collected species occurring in 63% of the samples, followed by *M. glabratus* in 44%, *A. variegata* in 35%, *S. bicarinata* in 31%, and *M. pusillus* in 25%. Less than 3% of samples included *D. parva*?, *O. trivittatus, S. lateralis,* or *Stenelmis* n. sp. *Pelonomus obscurus* was not collected during the study.

Excluding the coastal area south of Lake Pontchartrain, a general decrease in the number of species was noted from south to north, as well as east to west in the southern half of the state. Eleven species were collected in the 2 northernmost tiers of parishes while all 25 species occurred in the parishes to the south. Seven species of dryopoids are curiously absent from the northern quarter of the state but occur in central and west-central Louisiana: *E. thoracica, H. lithophilus, D. brevipennis, D. harleyi, D. parva*?, *Dubiraphia* n. sp. C?, and *S. antennalis.* The ranges of all of these species except *D. harleyi, Dubiraphia* n. sp. C?, and *S. antennalis* are known to extend north of Louisiana. There were no species unique to the northern part of the state.

LeSage and Harper (1975) concluded that latitude and physiography determined by underlying geologic formations were probably the major factors governing the distribution of dryopoid species in Quebec. They noted a decrease in the number of species from south-to-north, with 31 species occurring near the 45th parallel decreasing to only 2 north of the 50th parallel. It was also observed that Quebec's 3 major geologic regions each had a distinctive dryopoid fauna and water chemical characteristics. Mingo (1979), in a study of riffle beetle distribution in Maine, found that an interaction of latitude and altitude was responsible for observed patterns, with the effects of latitude similar to those noted by LeSage and Harper. All but one of 27 species occurred at the 45th parallel, decreasing to 10 species at about the 47th parallel in northern Maine. The north-south distributions of Louisiana dryopoids are somewhat similar to the latitude effects described by LeSage and Harper and Mingo. However, in Quebec and Maine it is likely that the species involved are at the northernmost limits of their ranges at those latitudes, and hence exhibit a south-to-north decline. In Louisiana the number of coastal plain species decreases northward as the Fall Line, which passes through southern Arkansas, is approached. All of the 6 coastal plain species in the state occur east of the Mississippi River, 3 of them occur west of the river in central Louisiana, but only 2, *S. grossa* and *Stenelmis* n. sp., reach the northern boundaries of the state. It would be interesting to know if a similar north-south trend occurs in Mississippi.

Twenty-four species were collected east of the Mississippi River and 19 west of the river. Fifteen were found in the westernmost parishes. Of the 6 found exclusively east of the river, 3 are coastal plain species and 3 are eastern species. All of these occurred solely in sandy/gravelly streams. Thirteen of the 19 species found west of the river were collected in the alluvial plain where streams are typically sluggish and mud- or clay-bottomed. Four of the remaining 6 species were collected only from sandy/gravelly streams; 2 were found both in sandy- and clay-bottomed streams. None were from streams with mud substrates. Because of lack of habitat diversity, it appears that the Mis-

TABLE 3. Frequency of collection of dryopoid species in the physiographic-vegetation zones of Louisiana from May 1979 to May 1981. * denotes non-study record.

SPECIES	% PINE-LANDS (N)	% OAK/PINE (N)	% UPLAND HARDWOOD (N)	% PRAIRIE (N)	% ALLUVIAL PLAIN (N)	% DELTAIC PLAIN (N)	Total N	# of Zones
E. thoracica	91.67 (11)		8.33 (1)				12	2
H. basalis	77.42 (24)	9.68 (3)	12.90 (4)				31	3
H. fastigiatus	92.86 (13)		7.14 (1)				14	2
H. lithophilus	78.57 (22)		17.86 (5)		3.57 (1)		28	3
P. obscurus					*	*	0	2
A. variegata	84.00 (42)	6.00 (3)	4.00 (2)		6.00 (3)		50	4
D. brevipennis	80.00 (16)		5.00 (1)	5.00 (1)	10.00 (2)		20	4
D. harleyi	40.00 (2)		20.00 (1)	20.00 (1)	20.00 (1)		5	4
D. parva?	100.00 (1)						1	1
D. vittata	82.14 (23)		3.57 (1)		14.29 (4)		28	3
D. n. sp. A?	85.71 (6)				14.29 (1)		7	2
D. n. sp. B?	62.50 (10)			18.75 (3)	18.75 (3)		16	3
D. n. sp. C?	85.71 (6)	14.29 (1)					7	2

G. dietrichi	87.50 (7)				12.50 (1)		8	2
M. glabratus	82.54 (52)	4.76 (3)	6.35 (4)		6.35 (4)		63	4
M. pusillus	83.33 (30)	2.78 (1)	5.56 (2)		8.33 (3)		36	4
O. trivittatus	100.00 (2)						2	1
S. antennalis	88.89 (8)	11.11 (1)					9	2
S. bicarinata	88.64 (39)	6.82 (3)	2.27 (1)		2.27 (1)		44	4
S. convexula	100.00 (9)				*		9	2
S. crenata?	83.33 (5)		16.67 (1)				6	2
S. grossa	66.67 (60)	14.44 (13)	2.22 (2)	3.33 (3)	13.33 (12)		90	5
S. lateralis	100.00 (1)						1	1
S. sinuata	70.00 (7)				30.00 (3)		10	2
S. n. sp.	*	33.33 (1)		33.33 (1)	33.33 (1)		3	4
# of Species (N = 25)	24	9	13	5	16	1		
% of Total	96.00	36.00	52.00	20.00	64.00	4.00		
# of Collections (N = 142)	102	14	6	4	16	0		
% of Total	71.83	9.86	4.23	2.82	11.27	0		

sissippi Embayment is a partial barrier to westward dispersal of riffle beetles in Louisiana. Species that prefer sandy/gravelly streams may not be able to disperse the 50-100 mi (80-160 km) distance across the Mississippi alluvial plain to suitable habitat. Findings in this respect agree with those of Bick (1957) and Louton (1975). Unfortunately, little information is available about how far aquatic dryopoids disperse.

Physiographic-Vegetation Zones.—The frequency of collection of species from 5 of the zones illustrated in Figure 1 are contained in Table 3. A total of 72% of the productive collections were from pineland streams, 11% were from the alluvial plain, and 10%, 4%, and 3% were from oak-pine, upland hardwood, and prairie areas, respectively. No dryopoids were found in the deltaic plain during the study; however, *P. obscurus* had been previously collected in the region. All of the sites sampled in the area were probably unproductive because of habitat unsuitability. Likewise, riffle beetles were not found in the Mississippi River alluvial plain in the northeast corner of the state above Avoyelles Parish despite several collecting attempts. This highly agricultural area has been known for extensive pesticide use in past years, a factor that may have eliminated or reduced dryopoid populations, if, in fact, they ever existed. There are 2 literature records from this area, *S. grossa* from East Carroll and Madison parishes (Table 1).

The species richness of zones can be compared by noting the total number of species occurring in each (Table 3). Non-study records, denoted by asterisks, are also shown. Twenty-four species have been collected in the pinelands, 16 in the alluvial plain, 13 in upland hardwoods, 9 in oak-pine areas, 5 in the prairie, and one in the deltaic plain. Only the pineland zone had unique species (*D. parva*?, *O. trivittatus,* and *S. lateralis*) not occurring elsewhere, but the sample sizes for these were very small (<3). The majority of collections of 20 other species were from the pinelands. Besides *P. obscurus, Stenelmis* n. sp. was the only species not collected in pine areas during the study. However, it has been taken at lights in the pinelands of East Baton Rouge, Livingston, and Morehouse parishes. *Stenelmis grossa* was found in all zones except the deltaic plain. *Pelonomus obscurus* has been collected by others in the alluvial and deltaic plains.

Although dryopoids are much less mobile than Odonata, a pattern of distribution strikingly similar to that noted by Bick (1957) was observed. Bick found that the greatest number of species occurred in pinelands, many exclusively, while only one was restricted to the delta and none to the prairie or alluvium. He also stated that the prairie, alluvial, and deltaic regions offered little variety in habitat and shared many of the same species. His conclusion that varied topography and habitat diversity in the pinelands are responsible for species richness seems applicable to dryopoids as well. However, the absence of all species except *P. obscurus* from the deltaic plain and the Mississippi alluvial plain south of Lake Pontchartrain is puzzling, since a few species do occur in similar lentic or very slow current situations elsewhere in the state.

Drainage Basins.—Species richness of basins (Fig. 2) can be compared by noting the total number of species (Table 4) that were collected in each. Non-study records, denoted by asterisks, are also shown. The greatest number of species, 21, were found in the Pearl

River Basin which has the second smallest land area, 2% (Table 2); *H. basalis, P. obscurus, D. parva*?, and *Dubiraphia* n. sp. C? were not collected. The second largest number of species, 20, were collected in the Lake Pontchartrain Basin. The only species not recorded there were *E. thoracica, P. obscurus, D. harleyi, D. parva*?, and *O. trivittatus. Ectopria thoracica* probably does occur in the basin since it was collected in the Pearl River Basin to the east and the Lower Mississippi River Basin to the west. Three basins had poor dryopoid faunas. No riffle beetles were collected in the Barataria Bay Basin during the present study, but an earlier collection of *P. obscurus* from the area was examined. Only *S. grossa* was collected in the Terrebonne Basin at sites located in the upper portion. Three species, *D. harleyi, Dubiraphia* n. sp. B?, and *S. grossa,* were recorded from the upper Atchafalaya River Basin. Twelve or more species occurred in each of the remaining basins except for the Upper Mississippi River Basin which was not sampled. One of the factors involved in the comparatively greater species richness of the Pearl River and Lake Pontchartrain basins is that they have 4 species (*G. dietrichi, O. trivittatus, S. convexula,* and *S. sinuata*) that are at the western limits of their ranges in the eastern "Florida parishes" and do not cross the Mississippi Embayment to the western basins. Habitat variety, discussed by Bick (1957) in reference to physiographic-vegetation zones, is probably also important in influencing the species richness of drainage basins. The Lake Pontchartrain Basin, with the second greatest number of species, had the greatest number of stream types or substrates (Table 2); only one or 2 substrates (mud and/or clay) were present in the relatively unproductive Atchafalaya, Barataria, and Terrebonne basins. In contrast, while only 2 substrates each were sampled in the Sabine (sand and mud), and Lower Mississippi and Pearl (sand and gravel) drainages, these yielded 12, 14, and 21 species, respectively. Therefore, it is apparent that more than just substrate diversity within basins is involved. The availability of microhabitats within the stream, related to stream type, is also undoubtedly a factor.

In reporting Oklahoma dryopoid records, Sanderson and Brown (1959) and Brown (1960) noted that each species had been collected in only one major watershed, and then usually just in a limited part, suggesting ecological differences in streams. In Louisiana it appears that while some species seem to be restricted to certain watersheds, others are widespread and occur in many. Table 4 gives the frequency of collection of dryopoid species within 11 of the state's 12 drainage basins, including non-study records denoted by asterisks. *Stenelmis grossa* was collected in 10 basins, followed by *H. lithophilus, A. variegata, D. vittata, M. glabratus, M. pusillus,* and *S. bicarinata* in 8, and *E. thoracica* in 7. The most restricted species were *D. parva*? in the Ouachita Basin and *O. trivittatus* in the Pearl Basin; *G. dietrichi, S. convexula, S. lateralis,* and *S. sinuata* were collected only in the Pearl and Lake Pontchartrain basins; *S. crenata*? was collected in all 3 basins of the "Florida parishes." *Helichus basalis,* a common species collected at 31 sites in 6 basins, was apparently absent from the Pearl River Basin although it occurs farther east in Alabama and west in Louisiana. Like *H. lithophilus,* it may be found with additional collecting.

In general, it appears that most Louisiana species do not exhibit watershed or drainage basin specificity. Essentially the same species are found

TABLE 4. Frequency of collection of dryopoid species in the drainage basins of Louisiana from May 1979 to May 1981. * denotes non-study record.

SPECIES	1[1] % N	2[2] % N	3[3] % N	4[4] % N	5[5] % N	7[6] % N	8[7] % N	9[8] % N	10[9] % N	11[10] % N	12[11] % N	Total N	# of Basins
E. thoracica			8.3 1		16.7 2	8.3 1	16.7 2	16.7 2	25.0 3	8.3 1		12	7
H. basalis			6.5 2	9.7 3		16.1 5	22.6 7		38.7 12	6.5 2		31	6
H. fastigiatus				14.3 2	*	14.3 2	28.6 4	28.6 4	14.3 2			14	6
H. lithophilus			3.6 1	25.0 7	7.1 2	17.9 5	10.7 3	*	28.6 8	7.1 2		28	8
P. obscurus		*	*		*	*						0	4
A. variegata			12.0 6	40.0 20	2.0 1	4.0 2	16.0 8	16.0 8	6.0 3	4.0 2		50	8
D. brevipennis			10.0 2	55.0 11	5.0 1	5.0 1		20.0 4		5.0 1		20	6
D. harleyi	20.0 1				20.0 1	20.0 1	20.0 1	20.0 1				5	5
D. parva?							100.0 1					1	1
D. vittata			14.3 4	42.9 12	3.6 1	3.6 1	3.6 1	21.4 6	3.6 1	7.1 2		28	8
D. n. sp. A?			14.3 1	42.9 3	14.3 1			14.3 1	14.3 1			7	5
D. n. sp. B?	6.3 1		12.5 2	12.5 2	43.8 7		12.5 2	12.5 2				16	6
D. n. sp. C?			28.6 2	14.3 1	14.3 1		14.3 1		14.3 1	14.3 1		7	6
G. dietrichi				12.5 1				87.5 7				8	2

M. glabratus			7.9 5	36.5 23	3.2 2	7.9 5	11.1 7	14.3 9	14.3 9	4.8 3		63	8
M. pusillus			5.6 2	27.8 10	2.8 1	5.6 2	22.2 8	27.8 10	2.8 1	5.6 2		36	8
O. trivittatus								100.0 2				2	1
S. antennalis			*	44.4 4			*	44.4 4		11.1 1		9	5
S. bicarinata			11.4 5	27.3 12	4.5 2	2.3 1	11.4 5	13.6 6	20.5 9	9.1 4		44	8
S. convexula				44.4 4				55.6 5				9	2
S. crenata?				16.7 1		33.3 2		50.0 3				6	3
S. grossa	1.1 1		11.1 10	14.4 13	13.3 12	2.2 2	21.1 19	6.7 6	23.3 21	4.4 4	2.2 2	90	10
S. lateralis				*				100.0 1				1	2
S. sinuata				10.0 1				90.0 9				10	2
S. n. sp.				*	100.0 3		*	*				3	4
# of Species (N = 25)	3	1	15	20	16	14	16	21	12	12	1		
% of Total	12.0	4.0	60.0	80.0	64.0	56.0	64.0	84.0	48.0	48.0	4.0		
# of Collections (N = 142)	2	0	13	33	13	8	21	17	28	5	2		
% of Total	1.4	0	9.2	23.2	9.2	5.6	14.8	12.0	19.7	3.5	1.4		

[1]1, Atchafalaya River
[2]2, Barataria Bay
[3]3, Calcasieu River
[4]4, Lake Pontchartrain
[5]5, Mermentau-Vermilion-Teche Rivers
[6]7, Lower Mississippi River
[7]8, Ouachita River
[8] 9, Pearl River
[9]10, Red River
[10]11, Sabine River
[11]12, Terrebonne

in the central and west-central parts of the state in the adjacent sections of 5 drainage basins, all of which are within the pinelands. The species assemblages in the 3 basins of the "Florida parishes" are similar, excluding those species which reach their western limits in the Pearl River and adjacent Lake Pontchartrain basins.

Seagle and Hendricks (1979) classified 15 dryopoids as upper and/or lower basin species in their study of the South Fork of the Shenandoah River Basin, Virginia. They found that 2 species, including *A. variegata,* were restricted to the upper basin and 2 to the lower basin; the remainder were nonspecific. A decrease in abundance and species diversity was also noted from upstream to downstream (1978). Likewise, Mingo (1979) divided the species in his study into upland, lowland, and generally distributed species. Although Louisiana exhibits little topographical variation, rolling uplands are present in the northern "Florida parishes" and in most of the west and central regions. The upper and lower portions of drainage basins can be delineated geographically. Several species have been collected only in the upper or upland regions of some or all of their basins. In the "Florida parishes," records of *H. fastigiatus, G. dietrichi, O. trivittatus, S. antennalis, S. crenata*?, and *S. lateralis* were clustered in the uplands of the 3 basins. Ten species were absent from the prairie region of the lower Mermentau-Vermilion-Teche Basin, but occurred in the pinelands of the upper basin and lower portions of adjacent basins: *E. thoracica, H. fastigiatus, H. lithophilus, A. variegata, D. vittata, Dubiraphia* n. sp. C?, *M. glabratus, M. pusillus, S. antennalis,* and *S. bicarinata.* In this case, however, it appears that absence is governed by the lack of suitable habitat in the prairie region rather than by preference for a particular section of the basin. Contrary to Young (1954), LeSage and Harper (1975), and Mingo (1979), *A. variegata* was not found to be exclusively an upland or upper basin species in Louisiana.

Seasonal and Monthly Occurrence

LeSage and Harper (1976a) reported a 3-4 year life cycle for 5 species of elmids in Quebec, with overwintering occurring in both adult and larval stages. Psephenid larvae and the adults and larvae of several elmid species were reported as occurring year-round in Wisconsin by Hilsenhoff et al. (1972). Similarly, adults and larvae have been collected in Louisiana during all seasons, although it is likely that subadult stages, and therefore life cycles, are shorter due to our mild climate.

Data representing monthly records for the species are contained in Table 5. As mentioned previously, results are probably biased towards the summer months of June, July, and August during which 62% of the sampling was done. Also, the most common species in the state, indicated by the number of sites at which each occurred, have the most complete monthly records. Thus, while the presence of a species is an absolute, its absence for a particular month may or may not be of significance.

Adult and larval dryopoids were collected during 11 and 10 months of the year, respectively. The adults and/or larvae of the following have been collected during all seasons: *H. basalis, H. fastigiatus, A. variegata, D. vittata, M. glabratus, M. pusillus, S. bicarinata, S. grossa,* and *Stenelmis* larvae. With the exception of *H. fastigiatus* and addition of *H. lithophilus,* these are also the most com-

mon species in the state, each occurring in more than 27 samples. Although January is devoid of species records, adults and larvae are undoubtedly present since samples including the following species were taken December 26, 28, and 29: *E. thoracica, H. basalis, H. lithophilus, A. variegata, M. glabratus, M. pusillus, S. bicarinata, S. grossa,* and *Stenelmis* larvae. *Dubiraphia* larvae were collected only from April to November; adults showed a similar concentration except for the record of *D. vittata* in February.

It seems likely that additional sampling in appropriate localities would verify year-round distributions for the aquatic adults and larvae of all species. However, adults appeared to be scarcer in the colder months because of depressed population levels and/or reduced activity.

Conclusion

A total of 5,688 specimens, 4,060 adults and 1,628 larvae, were collected and examined during the study. An additional 209 adult specimens and 19 larvae have been examined since then. Twenty-five species of aquatic Dryopoidea have been found in Louisiana, one psephenid, 4 dryopids, and 20 elmids. One of these, *Pelonomus obscurus,* was not collected during this study. Twenty-two species are reported in the state for the first time, including one undescribed species of *Stenelmis* and possibly 3 of *Dubiraphia.* Taxonomic problems involving Louisiana species exist in the genera *Dubiraphia, Stenelmis,* and perhaps *Microcylloepus.*

Thirty-six species of aquatic Dryopoidea have been reported from North and South Carolina (Brigham, 1982), 32 from Pennsylvania (Finni et al., 1978), 31 from Quebec (LeSage and Harper, 1975), 30 from Wisconsin (Hilsenhoff, 1975), 26 from Maine (Mingo, 1979) and California (Leech and Chandler, 1956), 22 from Oklahoma (Brown, 1956, 1960, 1966; Brown and Shoemake, 1964a; Sanderson and Brown, 1959), and 14 from Florida (Young, 1954). In studies of Dryopidae and Elmidae only, 24 species were recorded from Indiana (Finni and Skinner, 1975) and 23 from Kansas (Huggins, et al., 1976; Brown and Huggins, 1977). Eiland (1979) found 31 species of Elmidae in Alabama. Louisiana, with 25 species, apparently has a more restricted fauna than most of the states that have been surveyed. However, considering that the state lies within a single physiographic province and lacks the rocky streams which are reported to be choice riffle beetle habitat, the number of species occurring here is considerable.

The dryopoid fauna of Louisiana consists mainly of eastern and coastal plain species, 11 and 6 species, respectively. Two are distributed transcontinentally, while the ranges of the remaining 6 species are largely unknown. No western species were encountered. The records of 7 species may represent southward and/or westward range extensions; 4 of these are coastal plain species at the western limits of their ranges in the "Florida parishes." *Optioservus trivittatus* was found a considerable distance outside of its published range. *Stenelmis antennalis* is reported for the first time west of the Mississippi River.

The most common species in the state were *S. grossa* in 63% of the collections, *M. glabratus* in 44%, *A. variegata* in 35%, *S. bicarinata* in 31%, and *M. pusillus* in 25%. In general, the number of species decreases from south to north (excluding the deltaic plain) and from east to west in the southern half of the

TABLE 5. Monthly records of dryopoid larvae (L) and adults (A) in Louisiana from May 1979 to May 1981.

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	# of Months (L/A)
E. thoracica					L	L	L		L			L	5/–
H. basalis		A			A	A	A	A	A		A	A	–/8
H. fastigiatus		A		A		A	A	A	A				–/6
H. lithophilus						A	A	A	A	A	A	A	–/7
A. variegata		L		L/A	A	L/A	L/A	L/A	L/A	A	L/A	L/A	8/9
D. brevipennis				A	A	A	A	A	A		A		–/7
D. harleyi						A		A	A				–/3
D. parva?							A						–/1
D. vittata		A		A	A	A	A	A	A		A		–/8
D. n. sp. A?				A	A	A	A	A	A		A		–/7
D. n. sp. B?					A	A	A	A	A				–/5
D. n. sp. C?							A		A		A		–/3
D. spp. larvae				L	L	L	L	L	L		L		7/–
G. dietrichi				L/A	L/A		A	L/A					3/4
M. glabratus		L/A		L/A	L/A	A	L/A	L/A	L/A	L/A	L/A	L/A	9/10
M. pusillus		A		L/A	A	A	L/A	L/A	L/A			L/A	5/8
O. trivittatus				L/A			A	L/A					2/3
S. antennalis				A	A	A	A	A					–/5
S. bicarinata				A	A	A	A	A	A		A	A	–/8
S. convexula				A	A	A	A	A					–/5
S. crenata?		A		A				A					–/3
S. grossa		A	A	A	A	A	A	A	A	A	A	A	–/11
S. lateralis								A					–/1

S. sinuata		A		A			A	A					–/4
S. n. sp.					A	A		A					–/3
S. spp. larvae		L		L	L	L	L	L	L		L	L	9/–
Total Months													10/11
# of Taxa—A (N = 23)	0	8	1	15	14	16	19	21	14	4	10	7	
# of Taxa—L (N = 8)	0	3	0	7	5	4	6	7	6	1	4	5	
# of Collections (N = 142)	0	6	1	7	14	20	32	37	9	2	7	7	
% of Total	0.00	4.23	0.70	4.93	9.86	14.08	22.54	26.06	6.34	1.41	4.93	4.93	
# of Sites (N = 195)	5	7	2	8	20	37	42	41	10	4	8	11	
% of Total	2.56	3.59	1.03	4.10	10.26	18.97	21.54	21.03	5.13	2.05	4.10	5.64	

state, perhaps due to the northern and western boundaries of the coastal plain species. The Mississippi alluvial plain apparently acts as a partial barrier to westward dispersal of species.

The pineland physiographic-vegetation zone was the richest in number of species with 24, while 16 species occurred in the alluvial plain, 13 in the upland hardwoods, 9 in oak-pine areas, 5 in the prairie, and one in the deltaic plain. Habitat diversity resulting from a variety of stream types probably affects the species richness of zones in a positive manner.

The Pearl River and Lake Pontchartrain drainage basins had the greatest number of species, 21 and 20, respectively. This is probably partly due to the presence of a variety of habitats and microhabitats and partly to the fact that several coastal plain species are at the limit of their ranges in these basins and occur no farther west in the state. Six species were found exclusively in the 3 basins of the "Florida parishes" east of the Mississippi River. Only *P. obscurus* has been recorded from the Barataria Bay Basin and only *S. grossa* from the Terrebonne Basin. *Stenelmis grossa* occurred in 10 of the 12 basins, followed by *H. lithophilus, A. variegata, D. vittata, M. glabratus, M. pusillus* and *S. bicarinata* in 8, and *E. thoracica* in 7. Most species did not exhibit watershed specificity or upper/lower basin distinctions. Those restricted to a single basin had sample sizes of one or 2 collections only. Some of the species occurring in the "Florida parishes" were collected in the upland areas only.

Monthly data indicate that the adults and larvae of all species are probably present year-round in Louisiana streams.

The largest number of species were collected in streams with sand and gravel substrates. Excluding uncommon rocky streams, the smallest number of species were found in mud-bottomed watercourses. Many species exhibited microhabitat preferences. Future publications will further examine habitat and microhabitat selection by the aquatic dryopoids of Louisiana.

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APPENDIX I

Locations of Collection Sites

Current Louisiana Department of Transportation and Development

parish highway maps were used to determine the names of watercourses and the exact localities of sampling sites. If a name could not be found for a stream, it was referred to as a tributary (abbreviated "trib.") of a named watercourse. Major highway numbers and the nearest town are given from the Department of Transportation and Development 1979-1980 state road map. Compass direction of a site from the nearest town is straight line direction, not necessarily the direction on the highway given. Range (R), Township (T), and Section (Sec.) data are provided when the site was not on a numbered highway or was on a road not shown on the state road map. All collections were made by the senior author. Asterisks preceding stream or river names indicate that the site was unproductive. Numbers in parentheses—i.e., (1), (2), etc.—are given following the stream name when more than one site was sampled. This is necessary to clarify the species records presented in the Systematic Treatment. Boldfaced names refer to parishes.

ACADIA: Bayou Plaquemine Brule, N of Crowley on Hwy. 13; 10-VI-1980. Long Point Gully, S of Maxie on Hwy. 13; 10-VI-1980. **ALLEN:** Bayou Blue, N of Elton on Hwy. 26; 9-VIII-1979. Calcasieu River, NW of Oberlin on Hwy. 26; 30-VII-1980. Mitchell Creek, E of Oberlin E off US Hwy. 165, R3W T5S jct. Secs. 3 & 10; 9-VIII-1979. Soapstone Creek, W of Elizabeth, N off Hwy. 112 W jct. Hwy. 377, R6W T2S jct. Secs. 23 & 26; 30-VII-1980. Trib. of Calcasieu River, W of Kinder, N off US Hwy. 190 E of Calcasieu R., R5W T6S Sec. 29; 29-V-1979. *West Fork Caney Creek, S of Oakdale on Hwy. 372; 9-VIII-1979. **ASCENSION:** *New River, E of Gonzales on Hwy. 431 N jct. Hwy. 429; 6-XI-1980. **ASSUMPTION:** * Bayou Valerie, NE of Pierre Part on Hwy. 70; 18-VII-1980. **AVOYELLES:** Coulee des Grues, S of Marksville, W off Hwy. 115 just N Coulee des Grues bridge, R4E T2N Sec. 30; 4-IX-1980. **BEAUREGARD:** Bundick Creek (1), N of Dry Creek on Hwy. 113; 24-V-1979. Bundick Creek (2), E of DeRidder on Hwy. 112; 30-VII-1980. *Dry Creek, S of Dry Creek (town) on Hwy. 113; 24-V-1980. Hickory Branch, W of Longville on Hwy. 110; 31-VII-1980. Johns Gully, NE of Fields on Hwy. 109; 31-VII-1980. *Trout Creek, W of DeRidder on US Hwy. 190; 30-VII-1980. **BIENVILLE:** Cypress Creek, 7 mi (11.2 km) N of Mt. Olive on Hwy. 147; 16-VIII-1979. Leatherman Creek, NW of Gibsland on I-20; 15-VI-1980. Redfield Branch of Toulon Bayou, SW of Ringgold on Hwy. 4; 16-VI-1980. Sixmile Creek, SW of Bienville, W off Hwy. 9, R6W jct. T15N Secs. 1 & 2 and T16N Secs. 35 & 36; 16-VI-1980. **BOSSIER:** *Cypress Creek, 1.5 mi (2.4 km) E of Plain Dealing on Hwy. 2; 15-VIII-1979. Flag Lake spillway, Fifi Bayou, E of Bossier City on East Reservation of Barksdale AFB, R12W T18N Sec. 34; 28-XII-1979. Martin Creek, W of Springhill on Hwy. 157; 15-VIII-1979. *Trib. of Foxskin Bayou, E of Bossier City on East Reservation of Barksdale AFB, R11W T18N Sec. 30; 28-XII-1979. Trib. of Little Cypress Bayou, W of Bolinger on the Dogwood Drive S off Hwy. 537, R13W T23N Sec. 33; 14-VI-1980. **CADDO:** Cypress Bayou, S of Spring Ridge on Hwy. 789; 17-VI-1980. Flag Branch of Kelly Bayou Canal, S of Ida on US Hwy. 71; 14-VI-1980. Myrtis Mill Creek, N of Vivian at Myrtis on Hwy. 1; 14-VI-1981. Paw Paw Bayou (Quapaw Bayou), N of Greenwood on Hwy. 169; 17-VIII-1979. Shettleworth Bayou, W of Blanchard in Walter B. Jacobs Nature Park, N off Parish Rd. 4; 17-VII-1979, 29-XII-1979. **CALCASIEU:** Buxton Creek, S of DeQuincy, W off Hwy. 27, R11W T8S jct. Secs. 23 & 24; 31-VII-1980. Indian Bayou, N of Westlake, E off Hwy. 378 Spur, R9W T8S Sec. 26; 31-VII-1980. **CALDWELL:** Castor Creek, W of Grayson on Hwy. 126; 26-VII-1980. Trib. of Flat Creek, NW of Olla on Hwy. 127 just E of Winn P. line; 26-VII-1980. **CATAHOULA:** Bushley Creek, E of Manifest on Hwy. 8 just W jct. Hwy. 126; 25-VII-1980. Haggerty Creek, S of Duty, S off Hwy. 124, R5E T10N Sec. 11; 26-VII-1980. Trib. of Birds Creek, E of Manifest on Hwy. 8, 1.5 mi (2.4 km) E jct. Hwy. 126; 25-VII-1980. *Trib. of Bushley Bayou, S of Harrisonburg on Hwy. 124; 13-VI-1979. *Trib. of Little River, N of Jonesville on Hwy. 124; 13-VI-1979. **CLAIBORNE:** *Buck Creek, SE of Blackburn on Hwy. 2; 15-VI-1980. *Crows Creek, NE of Minden on Hwy. 518 at Webster P. line; 1-I-1980. Middle Fork Bayou D'Arbonne, SW of Colquitt on Hwy. 520; 17-VI-1979. **CONCORDIA:** *Trib. of Boggy Bayou, 1 mi (1.6 km) N of Slocum on Hwy. 15; 25-VII-1980. **DE SOTO:** Bull Bayou, SE of Stanley on Hwy. 174; 17-VI-1980. Caney Bayou, S of Kingston on Hwy. 175; 18-VIII-1979. **EAST BATON ROUGE:** Beaver Bayou, NE of Baton Rouge, SE off Hwy. 409 on Frenchtown Rd.; 21-XI-1980. Beaver Pond Bayou, NE of Indian Mound, SE off Hwy. 409, R2E T5S jct. Secs. 37, 58, 59, & 70; 20-XI-1980. Comite River (1), E of Zachary on Hwy. 64; 2-VII-1979. Comite River (2), SE of Baker, W off Hwy. 410 on Comite Dr.; 2-VII-1979. *Cooper Bayou, W of Zachary, W off US Hwy. 61 on Parish Rd. 6; 14-V-1980. *Corporation Canal, Baton Rouge, on South Campus Dr. at Louisiana State Univ.; 9-X-1980. *University Lake spillway, Baton Rouge, on Stanford Ave.;

9-X-1980. **EAST CARROLL:** *Macon Bayou, W of Gassoway on Hwy. 585 at W. Carroll P. line; 14-VI-1979. **EAST FELICIANA:** Amite River, W of Darlington on Hwy. 10 at St. Helena P. line; 28-VI-1979. Foster Creek, S of Jackson on US Hwy. 61; 14-V-1980. Hurricane Creek, 4.5 mi (7.2 km) W of Norwood, W off Hwy. 19, R1W T1S Sec. 58; 19-II-1980. *Little Sandy Creek, S of Clinton, E off Hwy. 67 at S boundary of Idlewild Expt. Sta.; 19-II-1980. Redwood Creek, Ethel on Hwy. 19; 3-VI-1979. Sandy Creek (1), S of Clinton, E off Hwy. 67 just S of Idlewild Expt. Sta.; 19-II-1980. Sandy Creek (2), S of Clinton, E off Hwy. 67 on Idlewild Expt. Sta.; 20-XI-1980. Woodland Creek, N of Woodland on Hwy. 67; 19-II-1980. **EVANGELINE:** Bayou des Cannes, NW of Chataignier on Hwy. 95; 22-VIII-1980. Bayou Grand Louis, SE of Ville Platte at US Hwy. 167 at St. Landry P. line; 22-VIII-1980. Bayou Nezpique (1), W of Bayou Chicot on Hwy. 106; 9-VIII-1979. Bayou Nezpique (2), W of Redell on Hwy. 376; 22-VIII-1980. **FRANKLIN:** *Pine Bayou Canal, Baskin on Hwy. 15; 27-VII-1980. **GRANT:** Big Creek, N of Pollock on US Hwy. 165; 9-VII-1980. Gray Branch of Fish Creek, NE of Dry Prong, S off Hwy. 123 on Forest Service Rd. 120; 9-VII-1980. Nantachie Creek, E of Montgomery on Hwy. 122; 20-VIII-1979. **IBERIA:** *Sandager Canal, SE of Olivier on Hwy. 182; 12-V-1981. **IBERVILLE:** *Bayou Tigre, SW of Bayou Goula on Hwy. 1; 12-V-1981. **JACKSON:** Trib. of Edwards Branch, 1 mi (1.6 km) W of Chatham on Hwy. 4; 16-VIII-1979. **JEFFERSON DAVIS:** Bayou Serpent and trib., N of Fenton on US Hwy. 165; 24-V-1979. Trib. of East Bayou Lacassine, 2.5 mi (4.0 km) N of Welsh on Hwy. 99; 24-V-1979. **LAFAYETTE:** *W trib. of Bayou Ile des Cannes, W of Scott on I-10; 10-VI-1980. **LAFOURCHE:** *Bayou Rond Pompon, W of Kraemer on Hwy. 307; 18-VII-1980. **LA SALLE:** Doyle Branch of Old River, 1.2 mi (1.9 km) W of Whitehall on Hwy. 460; 4-IX-1980. Hemphill Creek, E of Nebo on Hwy. 460; 4-IX-1980. Trout Creek, W of Jena on Hwy. 772; 9-VII-1980. **LINCOLN:** *Cypress Creek, NE of Vienna, E off US Hwy. 167 and S off Hwy. 822 on Parish Rd. 581; 17-VI-1979. Trib. of Choudrant Creek, NE of Choudrant on I-20 just E of Choudrant exit; 17-VI-1979. *Trib. of Cypress Creek, SW of Vienna, S off Hwy. 146, R3W T18N Sec. 9; 17-VI-1979. **LIVINGSTON:** Blood River, W of Albany on US Hwy. 190; 5-III-1980. Hog Branch, E of Livingston, S off US Hwy. 190 just E of Hog Branch bridge, R5E T6S Sec. 28; 2-VII-1979, 27-IX-1979. Little Colyell Creek, W of Frost, N off Hwy. 42, R4E T7S jct. Secs. 35 & 36; 6-XI-1980. *Little Natalbany River, N of Albany, W off Hwy. 1063, R6E jct. T5S Sec. 35 and T6S Sec. 2; 5-III-1980. Spillers Creek, NE of Watson on Hwy. 16 NE jct. Hwy. 1019; 13-VIII-1980. Trib. of Natalbany River, 0.8 mi (1.3 km) S of Springfield on Hwy. 22; 6-XI-1980. West Colyell Creek, NE of Denham Springs on Hwy. 1025; 20-XI-1980. **MADISON:** *Roundaway Bayou, S of Tallulah on US Hwy. 65; 14-VI-1979. **MOREHOUSE:** *Chemin-a-Haut Bayou (1), NE of Beekman, E off Hwy. 139, R6E T22N Sec. 2; 15-VI-1979. Chemin-a-Haut Bayou (2), NE of Beekman, E off Hwy. 139 on Hwy. 590; 28-VII-1980. *Coffee Bayou, E of Jones on Hwy. 835; 14-VI-1979. *Trib. of Bayou Bartholomew, NE of Beekman at Chemin-a-Haut State Park; 15-VI-1979. *Trib. of Chemin-a-Haut Bayou, NE of Beekman, E off Hwy. 139 on Hwy. 590; 15-VI-1979. *Williamson Creek, trib. of Snake Creek, N of Beekman on Hwy. 142; 28-VII-1980. **NATCHITOCHES:** Antoine Creek, S of Ashland on Hwy. 153; 18-VIII-1979. Bayou Pierre, Gorum on Hwy. 119; 26-XII-1980. Kisatchie Bayou, NE of Kisatchie, W off Forest Service Rd. 366 at Kisatchie Bayou Primitive Camp, R7W T5N Sec. 4; 3-IX-1979. Little Bayou Pierre, E of Kisatchie on Hwy. 118; 3-IX-1979. Malaudos Creek, S of Goldonna on Hwy. 156; 18-VIII-1979. Santabarb Creek, SW of Provencal, W off Hwy. 478, R9W T7N jct. Secs. 21 & 28; 10-VII-1980. **ORLEANS:** *Drainage canal, New Orleans, Joe W. Brown Memorial Park; 30-I-1980. **OUACHITA:** *Cypress Creek, S of Luna, S off Hwy. 557, R2E T15N Sec. 12; 17-VI-1979. Guyton Creek, S of Cadeville, N off Hwy. 34 on Parish Rd. 7; 16-VIII-1979. *South Cheniere Creek, S of Cadeville on Hwy. 34; 16-VIII-1979. **POINTE COUPEE:** *Bayou Fordoche, Fordoche on Hwy. 77; 20-XII-1979. Bayou Grosse Tete, E of Livonia on US Hwy. 190, 1.4 mi (2.2 km) W jct. Hwy. 1; 19-XII-1979. Bayou Latenache Drainage Canal, E of Melville on Hwy. 10; 26-VIII-1980. *Trib. of Bayou Moreau, W of Lettsworth on Hwy. 1; 20-XII-1979. **RAPIDES:** Castor Creek, SW of Alexandria, S off Hwy. 488 on Forest Service Rd. 273; 2-IX-1979. Hemphill Creek, W of Gardner on Hwy. 28; 8-VII-1980. *Horsepen Creek, SE of Libuse, S off Hwy. 1205, R2E T4N Sec. 19; 4-IX-1980. Spring Creek, S of Melder, S off Hwy. 112, R3W T2N jct. Secs. 35 & 36; 7-VII-1980. **RED RIVER:** Trib. of Black Lake Bayou, S of Womack on Hwy. 507 just S jct. Hwy. 514; 16-VI-1980. Trib. of Brushy Creek, S of Martin, E off Hwy. 507 on Hwy. 787; 18-VIII-1979. **RICHLAND:** *Muddy Bayou, E of Alto on Hwy. 15; 27-VII-1980. **SABINE:** Bayou Scie, NE of Zwolle on Hwy. 120; 10-VII-1980. Lewing Creek, E of Florien on Hwy. 118; 3-IX-1979. **ST. CHARLES**: *Trib. of Lanaux Canal, E of Boutte on US Hwy. 90 3.1 mi (5.0 km) E jct. Hwy. 3060; 18-VII-1980. **ST. HELENA:** Darling Creek, E of Chipola on Hwy. 38; 28-VI-1979. East Hog Branch, W of Montpelier on Hwy. 16; 13-VIII-1980. Tickfaw River, E of Montpelier on Hwy. 16; 13-VIII-1980. Twelvemile Creek, SW of Greensburg on Hwy. 37; 31-V-1980. **ST. JAMES:** *Drainage canal, SE of Sorrento on I-10 at Ascension P. line; 30-I-1980. **ST. JOHN THE BAPTIST:** *Mississippi Bayou, N of Reserve on I-10 4 mi (6.4 km) E of St. James P. line; 30-I-1980. **ST. LANDRY:** *Bayou Little Teche, SE of Port Barre

on Hwy. 472; 19-XII-1979. Bayou Mallet, W of Lawtell on US Hwy. 190; 22-VIII-1980. Bayou Petite Prairie, SW of Melville, NE off US Hwy. 71, R6E T5S Sec. 2; 26-VIII-1980. Little Wauksha Bayou, E of Beggs on Hwy. 10; 19-XII-1979. **ST. MARTIN:** *Bayou Martin, SE of Parks, E off Hwy. 347, R7E T10S Sec. 5; 12-V-1981. **ST. MARY:** *Bayou Patterson, W of Patterson on US Hwy. 90; 12-V-1981. **ST. TAMMANY:** Abita Creek, Abita Springs on Hwy. 435; 29-IV-1981. *Bayou Lacombe, NE of St. Tammany (town) on Hwy. 36; 29-IV-1981. Bogue Falaya River, E of Folsom, N off Hwy. 40, R10E T5S Sec. 11; 29-V-1979. East Bedico Creek, W of Covington on I-12; 18-II-1980. East Fork Little Bogue Falaya River, NE of Covington, just N off Hwy. 21 on Hwy. 1082; 29-IV-1981. Gum Creek, Pearl River (town) on Hwy. 41; 18-II-1980. Mill Creek, trib. of Bogue Chitto River, W of Bush on Hwy. 40; 20-VI-1979. Talisheek Creek (1), W of Talisheek (town), N off Hwy. 435; R13E T6S Sec. 9; 18-II-1980. Talisheek Creek (2), N of Talisheek (town) on Hwy. 450 Spur; 2-VII-1980. Tchefuncte River, NW of Folsom, W off Hwy. 450, R9E T4S Sec. 42; 29-V-1979. **TANGIPAHOA:** Big Creek, SE of Tangipahoa, S off Hwy. 440 on Hwy. 1054; 7-VIII-1980. Chappepeela Creek (1), SE of Loranger on Hwy. 40; 29-V-1979. Chappepeela Creek (2), E of Holton on Hwy. 16; 31-V-1980. Natalbany River, W of Independence on Hwy. 16; 13-VIII-1980. Selzers Creek, E of Ponchatoula on Hwy. 22; 6-XI-1980. Tangipahoa River, SE of Osyka, MS, on Hwy. 1054; 31-V-1980. Terrys Creek, Kentwood on Hwy. 38; 28-VI-1979. **TENSAS:** *Clark Bayou, SW of Newellton on US Hwy. 65 S jct. Hwy. 4; 14-VI-1979. *Lake Bruin, N of St. Joseph at Lake Bruin State Park; 14-VI-1979. **TERREBONNE:** *Drainage canal, E of Chacahoula parallel to Hwy. 20; 18-VII-1980. **UNION:** Bayou de Loutre, E of Spearsville on Hwy. 550; 28-VII-1980. Cypress Creek, SE of Spearsville on Hwy. 15 just S jct. Hwy. 550; 27-VII-1980. Little Corney Bayou, E of Lillie on Hwy. 15; 16-VI-1979. Meridian Creek, W of Marion on Hwy. 348; 28-VII-1980. *Middle Fork Bayou D'Arbonne, SW of Bernice, W off US Hwy. 167 on Parish Rd. 4416; 16-VI-1979. **VERNON:** Calcasieu River, N of Slagle on Hwy. 8; 8-VII-1980. East Anacoco Creek, E of Anacoco on Hwy. 111; 10-VII-1980. Liberty Creek, E of Leesville, S off Hwy. 468 on Castor Lake Rd.; 8-VII-1980. Sixmile Creek, W of Pitkin on Hwy. 10; 2-IX-1979. **WASHINGTON:** Bogue Chitto River, W of Warnerton on Hwy. 438; 2-VIII-1979. Bogue Lusa Creek, Sheridan on Hwy. 10; 30-IV-1981. Bonner Creek, S of Franklinton on Hwy. 25; 7-VIII-1980. Crains Creek, S of State Line (town) on Hwy. 62; 2-VIII-1979. Foster Creek, E of Angie, E off Hwy. 21, R14E T1S Sec. 51; 30-IV-1981. Hays Creek, E of Clifton on Hwy. 38; 7-VIII-1980. Lawrence Creek, N of Enon on Hwy. 16; 20-V-1979. Mill Creek, E of Enon at jct. Hwys. 16 & 60; 2-VII-1980, 7-VIII-1980, 13-IV-1981. Muster Ground Creek, W of Varnado on Hwy. 436; 30-IV-1981. North Carson Creek, W of Franklinton on Hwy. 450; 30-IV-1981. Pushepatapa Creek, W of Varnado, NE off Hwy. 436, R13E T2S Sec. 2; 2-VII-1980. Silver Creek, NE of Mt. Hermon on Hwy. 438; 2-VIII-1979. **WEBSTER:** Caney Creek below Caney Lakes, N of Minden, NW off US Hwy. 79/80 on Parish Rd. 1; 29-XII-1980. Cooley Branch, S of Minden on I-20; 16-VIII-1979. Holder Creek, E of Cotton Valley on Hwy. 3008; 29-XII-1980. Indian Creek, S of Shongaloo on Hwy. 2; 15-VIII-1979. *Trib. of Upper Caney Lake, N of Minden, R9W T19N Sec. 4; 1-I-1980. **WEST BATON ROUGE:** Bayou Poydras, W of Port Allen at jct. Hwys. 76 & 413; 26-VIII-1980. **WEST CARROLL:** *Little Colewa Bayou, W of Forest, N of jct. Hwys. 2 & 582; 28-VII-1980. *Trib. of Colewa Bayou, E of Jones on Hwy. 585; 14-VI-1979. **WEST FELICIANA:** Alexander Creek, St. Francisville on US Hwy. 61; 19-X-1980. Baker Creek, N of Weyanoke, NE off Hwy. 66, R4W T1S Sec. 73; 19-X-1980. Bayou Sara, NE of Weyanoke, R3W T1S jct. Secs. 69 & 71; 7-VIII-1979. *Sandy Creek, NE of Weyanoke, R3W T1S Sec. 61; 7-VIII-1979. Thompson Creek, W of Jackson on Hwy. 10; 14-V-1980. Tunica Bayou, N of Tunica on Hwy. 66; 7-VIII-1979. West Fork Thompson Creek, just E of Spillman on Hwy. 421; 3-VI-1979. **WINN:** E trib. of Kiesche Creek, NE of Winnfield on Hwy. 34; 13-VI-1980. Mill Creek, W of Calvin on Hwy. 156; 18-VIII-1979.

APPENDIX II

Additional Locality Records

Locality data (usually label data) are presented below for dryopoids collected outside of the study proper, i.e., before May 1979 or after May 1981, or collected by someone other than the authors. Records are from the Louisiana State University Insect Collection (LSUC), the University of Southwestern Louisiana (USL), and Harley P. Brown (HPB). Numbers in parentheses—i.e., (1), (2), etc.—following a location name are to clarify the species records presented in the Systematic Treatment. Boldfaced names refer to parishes.

ALLEN: Bundicks Cr. near Crosby L., 14-V-1977, K. T. Dupont (USL). **AVOYELLES:** Coulee des Grues, 3.2 km WSW of Marksville, 16-X-1981, C. B. Barr (LSUC). **BEAUREGARD:** Bundicks Lake, 19-IV-1973, J. Colley (Aq. In. Cl. 5) (USL). (Near Rosepine), 3-VI-1975 to 17-VI-1975, light

trap (LSUC). Whiskey Chitto Cr. 2 mi N Wye, 14-IV-1973 (Aq. In. Cl. 5) (USL). **BIENVILLE:** SE Arcadia on Hwy 147, 76/6/5, H. P. Brown (HPB). NE Bienville, 76/6/5, H. P. Brown (HPB). **CALCASIEU:** Sam Houston Jones St. Pk., 21-V-1982, E. G. Riley, blk. lt. (LSUC). **CATAHOULA:** Bushley Cr., LA 8 just W jct. LA 126N, 16-X-1981, C. B. Barr (LSUC). **EAST BATON ROUGE:** Baton Rouge (1), November (LSUC). Baton Rouge (2), 10-VI-1973, T. M. Andrews (LSUC). Baton Rouge (3), 6-28-1956, J. H. Roberts (LSUC). Baton Rouge (4), Burden Research Center, 11-IX-1974, 12-IX-1974, 13-IX-1974, light trap (LSUC). Beaver Pond Bayou, NE of Indian Mound, SE off Hwy. 409, R2E T5S jct. Secs. 37, 58, 59, & 70; 13-X-1981, C. B. Barr (LSUC). 1.2 mi S Central (1), E on LA 3034, 25-II-1978, Coll. C. B. Barr, swampy area (LSUC). 1.2 mi S Central (2), E of LA 3035, 28-V-1982, Coll. C. B. Barr, black light trap (LSUC). **EAST FELICIANA:** Idlewild Expt. Sta., 29-IV-1975 to 2-V-1975, 2-VI-1975 to 6-VI-1975, light trap (LSUC). Little Comite Cr., Hwy. 19, 16-IV-1983, T. W. Walker collector (LSUC). Sandy Cr. s Jackson, 76/6/26 (HPB). **EVANGELINE:** Bayou Cocodrie at dirt road below Glenmora and Turkey Creek, 18-III-1978, M. F. Vidrine (USL). **GRANT:** Big Creek, Pollock, 73/6/28, Bill Stark (HPB). 4-H Camp Grant Walker (E of Pollock), 28-VII-1982, C. B. Barr, blacklight (LSUC). Stuart Lake Rec. Area (Kisatchie Natl. Forest), 22-29-VII-1982, E. G. Riley, black light trap (LSUC). **IBERVILLE:** St. Gabriel Expt. Sta. (1), 18-VIII-1972, light trap (LSUC). St. Gabriel Exp. Sta. (2), 31-VII-1981, Coll. E. G. Riley, black light trap (LSUC). St. Gabriel Exp. Sta. (3), 2-VIII-1983, Coll. E. G. Riley, collected at blacklight (LSUC). **JEFFERSON:** Grand Isle, 6-24-42, 6-26-42, J. H. Roberts (LSUC). Grand Isle St. Pk., IX-5-1981, E. G. Riley, at light (LSUC). **LIVINGSTON:** Denham Springs, VII-11-1967, Liesel Klenk (LSUC). Hog Branch E of Livingston, 20-II-1983, T. W. Walker collector (LSUC). Little Natalbany River, Albany, 73/6/27, Bill Stark (HPB). Tickfaw River, Holden, 73/6/27, Bill Stark (HPB). Tickfaw R. W of Holden, 23-IV-1972 (Aq. In. Cl. 14) (USL). **MOREHOUSE:** Chemin-a-Haut St. Pk., 27-VII-1981, E. G. Riley & C. T. Robinson, collected at light (LSUC). **NATCHITOCHES:** Kisatchie Natl. Forest, Kisatchie Bayou Campgrd., 14-VI-1984, C. B. & J. E. Barr, mercury vapor & blk. lt. (LSUC). Little Bayou Pierre at LA Hwy. 118, 14-VI-1984, blacklight, Coll. C. B. & J. E. Barr (LSUC). Little Bayou Pierre 7 mi w Mora, 78/6/4, Jeff Witcosky (HPB). **RAPIDES:** Germany Branch, 70/11/30, Roy Rhame (HPB). Loving Cr. 2.8 mi SE of Castor Plunge, 21-III-1976, Tom Hardaway (USL). **SABINE:** 6 mi W Florien, V-22-82, E. G. Riley, blacklite (LSUC). **ST. HELENA:** Darling Creek at Hwy. 38 E of Chipola, 2-III-1979, J. T. Wassell (LSUC). **ST. MARTIN:** Parks, X-18-1962, Aithel McMahon (LSUC). **ST. TAMMANY:** Honey Island Nature Trail (Pearl R. Wildlife Mgt. Area), 17-VI-1982, black light, C. B. Barr & E. G. Riley (LSUC). I-10 at Pearl River, 17-VI-1982, black light, C. B. Barr & E. G. Riley (LSUC). Mill Creek at Hwy. 40, 11-II-1979, J. T. Wassell (LSUC). Tchefuncte River between Tangipahoa & St. Tammany parishes at Hwy. 40, 11-II-1979, J. T. Wassell (LSUC). **TANGIPAHOA:** Big Cr. 3+ mi E of Amite, 17-III-1973, R. Montegut; 24-IV-1976 (Aq. In. Cl. 2) (USL). Hamilton Cr. at Hwy. 1061 N of Wilmer, 2-III-1979, J. T. Wassell (LSUC). Tangipahoa R. at La. 16, 15-IV-1972 (Aq. In. Cl. 6) (USL). Creek w of Hammond, 66/6/19, H. P. Brown (HPB). **VERNON:** Anacoco Bayou at Hawk Rd., 18-III-1978, L. Dugas (USL). **WASHINGTON:** Hays Creek N of Franklinton, 22-IV-1972 (Aq. In. Cl. 11); 24-IV-1976 (Aq. In. Cl. 5) (USL). Tchefuncte R. at La. 16, 15-IV-1972 (Aq. In. Cl. 5) (USL). Junction La. 16 & La. 60, 15 Apr. 1972 (Aq. In. Class 3) (USL). **WEST FELICIANA:** 28-VII-1981, Coll. A. Linsey, Student Collector (LSUC). Thompson Cr. s St. Francisville, 76/6/2 (HPB).

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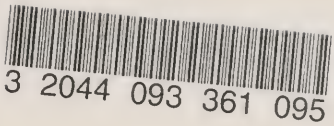
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